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A MANUAL
OF
HISTOLOGY.

BY

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OF VIENNA, AUSTRIA.

IN CO-OPERATION WITH

TH. MEYNERT, F. VON RECKLINGHAUSEN, MAX SCHULTZE, W. WALDEYER, AND OTHERS.

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PREFACE TO THE AMERICAN EDITION.

It has hitherto been customary among medical men to look upon Histology in very much the same light as music is looked upon by those interested in the subject of general education. They have considered it as an accomplishment requiring a great sacrifice of time and money, and yielding fruits in no wise proportionate to the outlay. There are signs, however, that this state of professional opinion is now rapidly passing away, and that this department will ere long be estimated at its true value, that is, as one of the corner-stones of the science of medicine. One institution of learning—I refer to the medical department of Harvard University—already now requires of its graduates an acquaintance with the principles of histology, and in this city there has been established for a little more than two years a laboratory where histological studies can be prosecuted under the guidance of competent instructors. Of still older date is the laboratory of the Army Medical Museum in Washington, which is devoted to histological purposes and is liberally supported by the United States Government. In all these institutions, however, the need of a text-book embodying the most recent discoveries, and setting forth the most approved methods of investigation, has been very seriously felt. No comprehensive text-book has ever appeared on the subject since the translation of Kölliker's Histology, which, though admirable as a work of reference for the advanced student, will scarcely be found to satisfy the wants of the beginner. For the present manual, however, it may fairly be claimed that it presents a most able and comprehensive review of what is known of histology. The name of Prof. Stricker, under whose guidance the work has recently been completed, is already familiar to the majority of American medical students as one of the foremost histologists in the world. Among the contributors to the manual are Von Recklinghausen, Rollett, Waldeyer, Max Schultze, and Meynert—men whose names alone are a sufficient guarantee of the high character of the work.

In regard to the translation, the editor would state that the first 406 pages are simply a reprint of Mr. Henry Power's excellent translation, published by the New Sydenham Society of London, in 1870. The remaining

chapters were translated by gentlemen of this city and Boston, whose familiarity with the subjects allotted to them specially fitted them for the work. In the case of Prof. Meynert's article on the Brain, the editor takes pleasure in stating that the translation of this very difficult chapter was intrusted to Dr. James J. Putnam, of Boston, at the special request of Prof. Meynert. Dr. Putnam was at that time a pupil in Prof. Meynert's laboratory, and as all doubtful points were referred by him to the author, the translation of this chapter may be relied on as an accurate reproduction of the author's views.

In the introduction of terms having a special technical meaning, the translators have endeavored to use the simplest form of Anglo-Saxon; where, however, a definite terminology had previously been used, no change has, as a general rule, been made.

The editor desires in this place to acknowledge his indebtedness to his coadjutors for the thorough and satisfactory manner in which they have done their work.

NEW YORK, July, 1872.

AUTHOR'S PREFACE.

No branch of science is being extended by such numerous and exact observations as Histology. While we enlarge the image upon the retina, through the agency of the microscope, we diminish the space momentarily brought into view, but we gain in exactness of definition what we lose in area. In the more delicate observations we make a very extraordinary increase in the exactness of our appreciation of light. After bringing the object to be examined into a condition answering special requirements, we concentrate our susceptibility to light upon one eye, and exclude all other outside disturbing influences: we further liberate this organ from any accessory effort; we do not turn it nor accommodate it; we take the ball, as it were, in both hands, substituting our adjusting apparatus for ocular accommodations, and movements of the object-slide for ocular motion.

Improvements in the microscope during the course of the last ten years have not only broadened the field of research to a great extent, but have also deepened it, and introduced better and more uniform illumination.

Histology is also extending in another direction. It is steadily mounting to a position among the comparative sciences. Under these circumstances it is continually becoming more difficult for any one individual to gain such a thorough acquaintance with its entire range as will fit him to prepare a conscientiously written text-book on the subject. In view of this fact I have undertaken to edit the present joint work. In accomplishing my object, the co-operation which has been afforded me by the best experts of our time, combined with the energy of the publisher, has enabled me to carry the work to a successful conclusion. It does not escape our notice, in glancing over the general outlines, that the appearance is not as smooth as if the whole had been the work of a single master. In some portions the results of years of industrious labor have gained a marked prominence. Intervening portions are sometimes the work of younger men.

There is no retouching, however, with which masters are fond of embellishing their works to suit our taste, and so keep the strong and weak elements of the production at an equal distance from the observer's eye.

I am confident my fellow-workers will sustain no loss from the roughness of framework; certainly not the best ones, for light has never yet been dimmed by less light; the younger men, too, will not complain if their share in the work be brought into notice.

The only remaining question now is, "Are our readers, or, which is more

important, is science to gain anything by it?" Both questions are practically one, for certainly, if we consult the interests of our readers, what better can be offered than that which best answers the demands of science? In short, we need no argument to show that the true relations of objects are best defined when there is absence of ornamentation.

It is impossible to deny that the painter's brush is still playing an important rôle in making text-books on animal tissues. Our knowledge in this field is but fragmentary, and we are only too apt to allow theories instead of facts to conceal our deficiencies.

Nor is the present work quite free from these features, though they are not so prominent, since the articles take the character of monographs; and there is, further, a merit connected with this latter fact, in so far as a single pervading method is avoided.

Now this same diversity in treating the various subjects is not the least advantage of our work. It thereby approaches nearer what should be the aim of a manual which is to furnish a statement of doctrines as they are, at a given period. Such statements, however, come nearer actual truth when there is no predominance of individual views.

On the other hand, multiplicity of workers has brought with it an evil. Some have opposed others upon points that are sometimes essential. This circumstance, I am certain, will only annoy those who value truth less than the convenience with which they store away the information they gain; for scientific men, and those who aim to be such, will certainly be glad that I have given space to any conflicting opinions.

"Opposition fosters the spirit of inquiry." *

S. STRICKER.

* "Durch den Widerspruch wird der Geist der Prüfung genährt."

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INTRODUCTION.

GENERAL METHODS OF INVESTIGATION.

By S. STRICKER.

The microscope is a means of research. When objects are so small that at ordinary distances from the eye they no longer produce sufficiently large images on the retina, they require, for their examination, either a simple or a compound microscope. The domain of investigation embraced by this instrument, however, does not limit research. Microscopy defines no doctrine, but is simply a method of examination; yet it is the most delicate with which we are acquainted for terrestrial objects, because modern microscopes are the most perfect of all optical instruments.

Up to the present time the microscope has been chiefly applied to the investigation of the various organisms; and our knowledge of the finer structure of plants and animals, and especially of the latter, has assumed the character of an independent science, which again presents important subdivisions. The observation of healthy tissues, and of those modified by, or originating in, disease, already constitutes the basis of two separate but closely allied departments of science, each of which can again be regarded from different points of view. We can, for example, push our inquiry either into the morphology or into the biology of the tissues; or, as it may be otherwise expressed, into the normal or pathological anatomy and physiology of the tissues. At present, however, the morphology and physiology of the tissues are so intimately connected with each other that no line of demarcation can be drawn between them. The observation of the vital phenomena presented by the tissues, and the experimental investigation of their properties, conducts us, in many instances, to a knowledge of the most delicate structural arrangements; whilst the converse always holds true, that a thorough knowledge of structure furnishes the key to many vital phenomena.

The technical methods of research applicable to these two subjects are nevertheless different. When we desire to follow, and ultimately to modify, the vital processes under the microscope, other means of research are required than when we merely wish to acquaint ourselves with the forms of the elementary parts. Moreover, experiments which are performed under the microscope differ according to whether they are conducted on living or on dead bodies. The sensitiveness of the former to external influences, makes—even in the microscopically small compass of the instrument, and

bearing in mind the management necessary for its use—experiments possible under circumstances which are not practicable in the case of dead tissue. Thus we find that changes can be induced in living tissue by slight variations in temperature, by feeble currents of electricity, and by weak solutions of acids; whilst the operation of these agents must be much more energetic for the purpose of experiment on the dead body, and this is not always agreeable for the observer, nor suitable for the more delicately constructed instruments. The greater sensitiveness of the living organism demands proportionate delicacy in its treatment, but at the same time facilitates experiment; and to this we may ascribe the circumstance that experimentation on the living body has gained so much in value during the last few years, that is, during the period that the investigation of living tissues has been so extensively undertaken.

The tissues may either be examined by the light which they reflect from their surface, or by that which passes through them—by direct or by transmitted light. Every object can be examined by direct light, provided that the degree of illumination from without, and its own power of reflecting light, are sufficiently great, and that both the object and the instrument can be fixed.

It is self-evident that the instrument must be capable of being focussed, or it would be impossible for trustworthy retinal images of various objects to be obtained. The examination of an object cannot be conducted by direct light with high powers, because the employment of such powers necessitates the close approximation of the lens to the object, whereby the latter is covered, and its illumination prevented. It is, however, possible to apply here the principle of the ophthalmoscope, and then this difficulty is overcome.

Examinations conducted by means of direct light are greatly assisted by direct illumination, or, what is still better, by throwing a pencil of rays on the part of the object to be illuminated; details then frequently become apparent which can scarcely be detected with the mere diffused light of day.

If examinations by means of direct light are undertaken at greater distances—as when, for example, lower powers are employed, or when the objects are examined or are prepared in a fluid—it is advantageous to use Brücke's doublet. This is placed in the arm of a Nachets' or Hartnack's stand, and the object is placed on the stage. The focussing can then be easily accomplished with the unassisted hand by moving the lens. This combination is very serviceable for preparations that have been teased out with needles, as in the isolation of ganglion cells and the separation of fine fibres. The object is in every instance placed on an opaque ground: if it be dark, upon a dull gray; and if clear, upon an opaque black ground. The object requiring to be isolated should in all instances be laid on a slide of polished glass, beneath which again may be placed a piece of dull white or black paper, as may be most convenient. For the examination of larger portions of tissue in fluid, little shells may be used, resting on a plane base, and having a spherical hollow, resembling an ordinary glass salt-cellar. A dull opaque ground may easily be obtained by covering the surface of the glass with a thick layer of colored wax or gutta-percha, which has the advantage of enabling the objects to be fixed in position by transfixion with needles.

If it be required to bring the object into strong relief, in order to examine the details of the surface, the lenses of Steinheil of München are especially to be recommended. It is advantageous, however, to attach them to an arm moving on a ball and socket joint, which again plays, horizontally and vertically, on a fixed vertical support. When it is required to

manipulate with forceps and scissors under still higher magnifying powers, the little preparation cell should be fastened upon a blackened wooden block, several centimetres in height, and resting on the table. The arms, being thus in a nearly horizontal position, and well supported, permit the observer to work with greater steadiness. In making preparations with strong lenses, the nose of the observer necessarily comes into close proximity with the object, and the bridge of the nose can be used as a point of support for the cutting instrument employed. When sections are made with scissors and forceps under strong lenses, it is usually necessary that the object should be firmly fixed, and, at the same time, very steady movement on the part of the cutting instrument is required. It is in particular quite indispensable that some kind of support should be given, if it be required, to make clean and thin sections of small and delicate objects.

If the left eye be applied to the lens, the right hand can with great certainty direct a fine pair of scissors balanced on the bridge of the nose whilst the left hand fixes the object. For the fixation of very delicate objects, substantial forceps, with very sharp, smooth points, will be found serviceable. If it be desired to work by means of direct light with a compound microscope, weak objectives, such as No. 5 of Hartnack's microscope, or those corresponding to them of other instruments, can alone be employed. Formerly weak compound microscopes, which gave erect images, were used for the preparation of objects. These so-called dissection microscopes are not, however, really necessary, since the opposite movement of the hand demanded for the inverted image is soon acquired by practice.

The examination of objects can, in like manner, be undertaken with transmitted light, both with the aid of simple and of compound microscopes. In regard to the use of the former, there is little to be added to what has already been said. For the examination of objects with transmitted light, it is obvious that the support must be transparent, and the objects must themselves be illuminated by the reflected light proceeding from either a mirror or a prism. Simple microscopes, or the lower powers of compound microscopes, can only be used with transmitted light, when general views of the topographical relations of the tissues to one another are desired. The larger the object, the lower must be the magnifying power employed, in order that a general view of it may be obtained. With such large objects it is usual to examine them in the first instance with a low power, and then to investigate the details of each part with a higher power. The very powerful lenses lately manufactured by Hartnack are extremely well adapted for the investigation of the living tissues, or of the well-preserved and isolated elements of the tissues. In specimens which have been roughly treated and are consequently not in a very fit state for microscopic research, as in those that have been hardened with re-agents, or stained with coloring matters, and repeatedly washed, very high powers are in the first instance less instructive than lower ones; indeed, those who are not very expert in the use of the instrument can actually see less with a No. 15 than with a No. 8 Hartnack. However, the highest powers are even here very serviceable to the beginner, if he be engaged in the definition of the deeper lying tissues. It is only requisite to use the fine adjustment with extraordinary care, to turn the screw with great gentleness; so that a fresh field is obtained, which may remain for some time under observation prior to passing to a greater depth, or returning to a more superficial part.

But if well isolated and well preserved morphological elements are under observation, and if the tissues are examined whilst still fresh, and without the addition of any fluids, or only of those which occasion no change in

them, the highest powers prove of the utmost value. The advances that have been made in our knowledge of cells and of the finer structure of nerve fibres are the result of researches undertaken with the admirable instruments that have recently been constructed. The value of these high powers is strikingly illustrated by the investigations on the living cornea, conducted by Recklinghausen and Kühne. It is indeed true, that in the perfectly fresh state, the structure of the cornea cannot be satisfactorily ascertained, even with the best glasses. In this state only those morphological elements are to be distinguished which refract light differently from the surrounding parts, and thus it happens that when fibres or cells are imbedded in connective tissue, or in fluids, the refractive power of which is the same as their own, they cannot be perceived even with the best glasses, and artificial means must be resorted to in order to render them visible. These may either be mechanical, effecting the separation and isolation of the morphological elements, or chemical, which dissolve the connecting material, or act differently upon it than upon the morphological elements. The best artificially prepared specimens, however, cannot supply the advantages of examination made on fresh preparations with magnifying powers of from 1,000 to 1,500 linear. Those outlines which can be distinguished in the living tissue, exhibit, besides sharpness, a certain softness, which renders their definition easy and pleasant. The naturally present cavities and fissures, in consequence of the different refractive power of their contents, differentiate themselves from the surrounding material with extraordinary sharpness. Lastly, outlines are distinguishable during life, which completely vanish after death. Even if these can be again rendered visible by the application of peculiar re-agents, their full significance is only to be recognized by our knowing that they are naturally present.

In the present condition of our instrumental means of research, it appears to be advantageous to commence histological studies by means of general topographical examination of the tissues with lenses of low powers; then to proceed to the examination of specimens that have been subjected to manipulation with lenses of moderate power, in such cases applying the stronger lenses only as a means of control for the penetrating powers of the weaker ones; and finally to proceed to the examination of the fresh tissues with the best means at our command.

I can attribute no very high value to the binocular (double-tubed) stereoscopic microscopes, so far as their use has at present extended. As yet they have only been employed with low powers. The relief of different parts of an object can be very well ascertained, even with a simple microscope, by merely varying the inclination of the head.

The simplest, but at the same time the most certain and elegant, mode of investigation with the compound microscope is to place the object in the centre of a smoothly-polished slip of glass, covering it with a thin quadrangular and also perfectly clean glass plate. The little glass plate, called also the glass cover, should lie with its surface parallel to the glass slide, a position which can only be attained when the object to be examined has been greatly and equally extended. Irregularly shaped and thicker masses interfere with the examination, because they make the glass cover assume an oblique position. If the tissue to be examined is diffused through a fluid, a drop should be placed on the glass slide; the cover should then be brought down to the upper surface of the drop, and cautiously allowed to fall by its own weight. By this means the inclusion of air bubbles is avoided. If the investigation is about to be continued for some time, or if it be desired that the medium in which the object lies should not become concentrated by evap-

oration from the edges, a brush dipped in oil may be drawn round the margin of the covering glass, which will effectually prevent it. If, after the glass cover has been applied, a portion of the fluid about to be examined exudes from the edges, so that the cover slips with an unsteady movement over the surface, a little piece of filtering paper may be employed to remove the excess of fluid, and the oil may then be applied. By this means the simplest kind of moist chamber may be made.

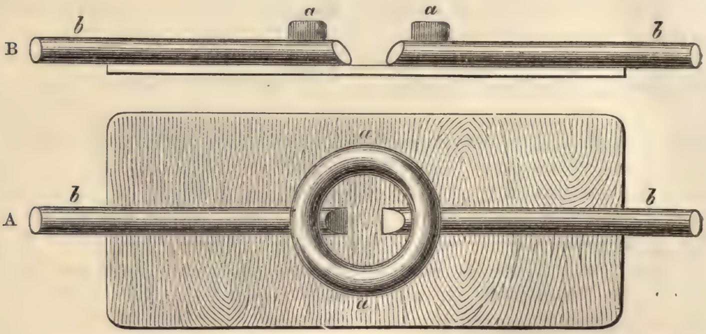
Recklinghausen first introduced the use of the moist chamber. The guiding idea of this was, that the object should be placed in a space in which the air was saturated with moisture, and this appeared to be so much the more important when it was found desirable to examine objects without a covering glass. In such cases the object is, of course, partially in contact with the air, and must necessarily give off watery vapor, unless the air be itself saturated with moisture.

But if we consider, on the other hand, that the precipitation of watery vapor from an atmosphere saturated with it upon such an object is dependent on temperature, it is easy to understand how difficult it is to obtain the exactly intermediate point in which water is neither given off nor taken up. Any imperfections in this respect, however, will increase with the capacity of the space by which the object is surrounded. It should, therefore, be made as small as practicable, and, if possible, altogether dispensed with; in other words, where practicable, only a covering glass should be used, the edges of which are oiled. The pressure which this exercises on the object is unimportant, and may, indeed, easily be avoided altogether; for it is only requisite to form an outside wall with oil, and to place a small quantity of the fluid within the space thus enclosed, before applying the covering glass, in order to protect it entirely from the weight of the latter. Circumstances may exist, however, which render it necessary that the preparation should be exposed to the air. It may, for instance, be requisite to ascertain the influence of various gases; in these cases a chamber must be used, of as small a size as possible, except where some special arrangements are made, enabling the amount of watery vapor present to be regulated. I employ for this purpose a ring of putty, varying in thickness according to circumstances; the object is then to be attached, as usual, to the lower surface of the covering glass; this is now to be brought down upon the ring of putty, and to be gently pressed down on the object with the handle of the scalpel. A drop of water placed upon the side is sufficient to saturate the space with aqueous vapor, and to prevent the object from drying. Great caution must, however, be used; for it will be found that the dry, smooth, polished covering plate becomes immediately tarnished when it is placed on the wall of putty. The drop of fluid should, therefore, only have a small surface, in order that it may not evaporate to too great an extent, and, on the other hand, it should not be too small, lest the object dry with too great rapidity. It is obvious that small variations in the proportion of water in the object are unavoidable.

A moist chamber formed in this fashion can easily be converted into a so-called gas chamber. In that part of the soft wall of putty which corresponds to the middle line of the glass slide, a small glass tube is to be introduced on each side, and to these caoutchouc tubes can be attached, which can be closed by bull-dog forceps when the passage of gas is not required. But when gases are to be transmitted, the necessary communications can be made through the caoutchouc tubes, and the forceps removed. This temporary and easily deranged chamber will not prove satisfactory to those who are constantly working with gases; by them it will be found better to ce-

ment the connecting tubules of glass once for all into grooves cut in the slide. The spaces left can be filled up with putty.

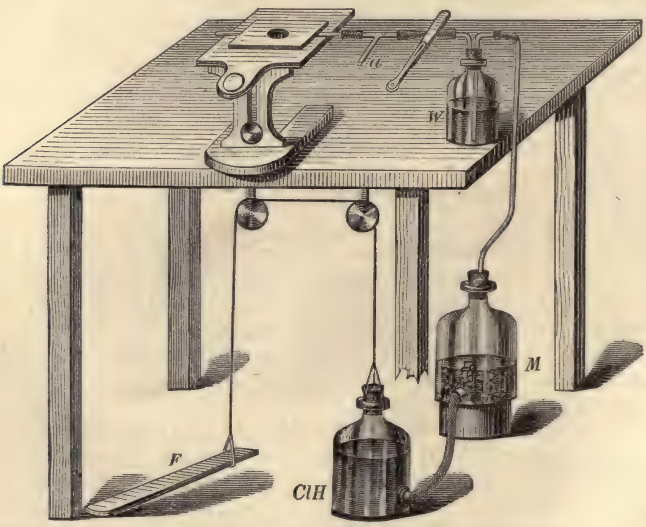
Fig. 1.



Gas chamber, natural size. A, bird's-eye view; B, longitudinal section through the middle line; *a a*, wall; *b b*, conducting tubes.

A slide which is to be used for such investigations with gas must be attached to the stage of the microscope, because the conducting tubes pull upon it, and so render the object liable to be displaced. The gas should be transmitted from washing flasks fixed on the stage, so that there may be firm supports between them and the microscope, whilst they are themselves connected with gasometers at some distance from the stage. In my own

Fig. 2.



investigations, in order to be able to dispense with the services of an assistant, and use both my hands at the stage for microscopic purposes, I have arranged my gas apparatus beneath the table in such a way that I can effect the passage of gas in one direction or the other by means of a treadle. If,

for instance, I wish to transmit carbonic acid gas, I so arrange the apparatus, shown in fig. 2, that the flask containing hydrochloric acid gas can be raised by a string attached to the treadle, and passing over pulleys. From the evolving flask M a caoutchouc tube leads to my fixed wash bottle W, and from this another tube passes to the microscope. The conduction of carbonic acid to an object under the microscope renders it requisite that we should be able to exchange it at will for atmospheric air. I introduce, therefore, between the wash bottle and the slide a T-shaped tube (*a*, fig. 2). The horizontal portion of this tube lies in the axis of communication between the wash bottle and the slide; whilst the cross-piece is directed towards the observer. A long caoutchouc tube is attached to the latter, which is seized by the observer between his teeth.

Between the T-tube and the wash flask W, a clip is introduced. When I open the clip,* and by means of the treadle F raise the flask containing acid, and thus cause carbonic acid to flow into the wash flask, and at the same time compress the caoutchouc tube between my teeth, the gas must pass over the slide; but if I apply the clip, and inspire through the tube in the mouth, I then draw in free air from the opposite end of the chamber. By this arrangement common air can be exchanged at will for carbonic acid gas, without interfering with the observation, and at the same time the hands are left free for any manipulation that may be requisite. A second apparatus, the so-called DEVILLE's, is arranged for the preparation of hydrogen beneath my table in the same manner as that above described. I use this gas as an indifferent medium; and, as it passes through a wash flask, mingle with it various vapors, as those of ammonia, chloroform, etc. The mixture is accomplished by the aid of a bag, which can be compressed with the foot, and from which a tube conducts into the wash flask. If the effect of pure hydrogen gas is desired to be seen, the above-mentioned gas chamber is insufficient. Kühne, to whom we are indebted for making the first investigations with gas chambers, employs a mercurial valve. Adopting this principle, I take a slide made of hard caoutchouc, which is perforated in the middle, and to the surface of which a glass plate is cemented; or, which comes to the same thing, I take a ring of hard caoutchouc, and

Fig. 3.

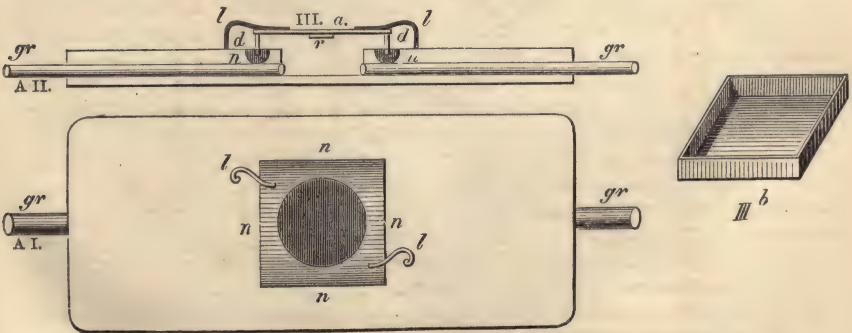


Fig. III. *a*, Gas chamber, with mercurial valve, natural size. A I, bird's-eye view; A II, longitudinal section through the middle line; *n n*, groove; *l l*, clips; *gr*, gas tubes; *r*, object; *d d*, covering glass in section. Fig. iii. *b*, covering glass.

* The use of the clip may be dispensed with if the column of water in the wash flask is high.

cement it to a glass plate. A groove is now made round the perforation, which can be filled with mercury. The cover glass must then be cemented to a little cell (fig. 3, *b*.).

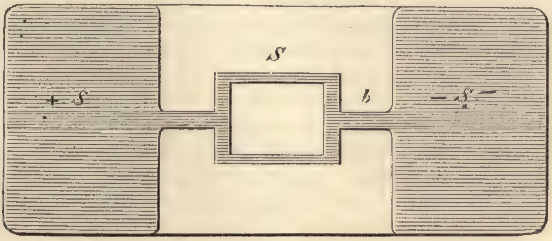
The object is placed on the inner surface of the cell thus formed, and the lateral walls of the cell are placed in the groove, dipping, therefore, into the mercury. If the cover glass is now kept down by clips, the gas chamber will be perfectly closed; and no further explanation is required to show how the gas, whose effect is to be. examined, may be conducted over the object.

There are certain difficulties accompanying the examination of objects in gas chambers; taking the simplest case for example, a drop of blood is placed on the lower surface of the cover, which is then laid on the cell, and firmly luted to it. The first current of gas which passes over it dries up the edges of the blood spot, and this can scarcely be avoided. It becomes necessary, therefore, to experiment with great rapidity in the gas chambers, or to add some indifferent fluid to the preparation, which may saturate the air contained in the little cell with aqueous vapor without essentially altering its character. But we are thus no longer working under the simplest conditions, and due allowance must be made for this in the conclusion at which we arrive.

The employment of the moist chamber is rendered still more difficult, if it be desired to warm the object whilst under observation with the microscope. Rollett was the first to introduce a means of varying the temperature in microscopic investigation. Max Schultze made improvements in this direction, and has constructed a stage capable of being heated, which can again be fitted to the stage of a microscope, is capable of being warmed throughout its whole extent, and can furnish the means by which the temperature of the object under examination can be varied at will. Various modes have since been suggested, by which the effects of elevation of temperature upon an object can be ascertained. In Max Schultze's stage, the mode of warming consists in the direct conduction of heat through metal plates. The attempt was subsequently made to conduct a warm fluid through the object stage, and still more recently, to employ warm vapor with the same object in view. A better method than any of these, and which demands attention as a means of heating the stage, consists in the conversion of a constant current of electricity into heat. In microscopical investigation, only a very small absolute quantity of heat is required, and indeed it is not necessary to warm the stage in its whole extent, but only its centre; or, what is still better, the glass cover placed on a slip of caoutchouc. An amount of heat so small as this we may reasonably expect to obtain from the interruption of even feeble currents of electricity. It is well known that the heating of a wire, introduced into the arc of a constant current, increases with the diminution in diameter of the wire; and indeed, according to Riess, in the proportion of the bi-quadrate of the diameter. For this purpose, therefore, we employ a proportionately thin wire, attached to the centre of a glass plate, the ends being in connection with the electrodes of a constant battery. When the current is closed, the temperature of the centre of the glass plate is raised. The attachment of the wire presents, however, certain inconveniences; and we possess in tin-foil a more appropriate means at our disposal. I am accustomed to cut the tin-foil into the form represented by S in the adjoining figure, and then to glue it to a glass slide; if now the extremities of the tin-foil are introduced into the arc of a constant current, the end in view is at once attained. A very convenient method of introducing the slide into the current is to at-

tach to one of Hartnack's microscopes a couple of brass springs, by which the preparation can be firmly clipped. These springs (D D, fig. 5), which are attached to holes in the stage by means of brass pins, are provided also with india-rubber pins, by which means they are isolated from the microscope. When they firmly clip the slide, they at the same time press on the broad end of the tin-foil s. It is then only requisite to attach a conduct-

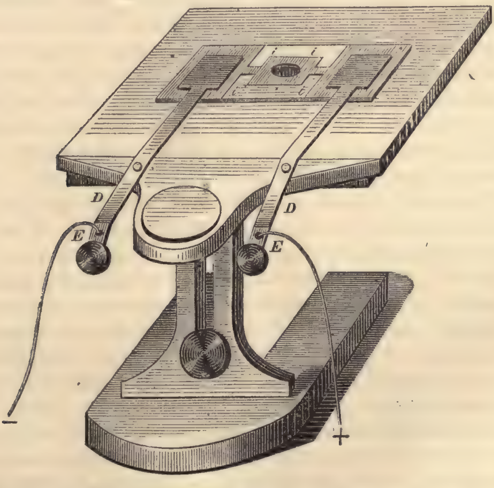
Fig. 4.



Slide adapted for being heated by means of electricity. Natural size.

ing wire at any point of each spring (E E, fig. 5), and the circuit will be closed by the tin-foil. A second strip of tin-foil, of the same breadth as that attached to the slide (*b*, fig. 4), is wound round the bulb of a thermometer, and introduced into the circuit at any convenient point. This furnishes the means of correctly estimating the temperature attained by the

Fig. 5.



Foot and stage of one of Hartnack's microscopes.

centre of the slide, when all the secondary conditions are uniform. These latter can, however, be estimated by comparison, and the due employment of a thermometer,—a proceeding that is always requisite, whatever may be the mode of heating employed. In order to accomplish this, at the point

where the object is situate, a fatty substance, the melting-point of which is known, should be placed, and the reading of the mercury should be taken at the moment that the fat begins to melt. The quantity of fat that is introduced should be very small, and should be in the field of the microscope. It will be found most expedient to cut a little disk out of the fat, to cover it dexterously, to watch it with a lens, and to calculate it accordingly.

I also apply one of Meidinger's chains with amalgamated zinc plates. A chain of this kind works with very great steadiness, if fed with regularity. It can be left closed for several days, and yet the temperature of the tin-foil kept to a definite degree, not varying with that of the room. It seldom requires water, but crystals of copper must be supplied at least once a day, so that the solution may be constantly and equally saturated. If we overlook, however, these slight drawbacks, and reflect that such precautionary measures are only requisite in cases where it is wished to maintain a particular preparation at a uniform temperature for many days and nights, we shall feel that in the interest of such important investigations it can scarcely be thought too great a trouble to attend at least once a day to the requirements of the machine. If the amount of work performed by the battery be but small, or if it be only occasionally applied, it will then long retain its activity without requiring other addition than that of a little water from time to time to supply the place of that which is lost by evaporation.

Meidinger's arrangement gives off no injurious vapors, and may therefore be enclosed in a little box, and placed beneath or near the work-table. I transmit the conducting wires through holes bored in the table, and when required for use, fasten them to the points indicated by + and — in fig. 5.

Inasmuch as the temperature of a thin wire introduced into a thicker arc is inversely as the square of this wire, whilst its length, when small, is of no importance, it follows that the method of measurement formerly employed is justified. But it is also clear that the active force present can be accurately accommodated on the basis of this law. For if the temperature diminishes as the square of the strength of the current, this decrease can, to a certain extent, be covered by diminishing the transverse section of the tin-foil, so that if a weak current be in use, the strip of tin-foil must be made proportionately narrow. As these strips are easily torn, I am accustomed to glue the tin-foil upon thin paper, and then cut out a very long strip with its central window. The larger portion of the strip I twine round the bulb of a thermometer in such a way that after making several coils, the two ends hang free. I then cover the whole bulb with a layer of shellac or glass cement, and pass it through a cork into an empty vessel, so that the ends of the tin-foil project. No special expertness is then required on the part of the experimenter to introduce these into the arc of the current. The bulb can also be so placed in front that its readings can be readily taken. The shorter end of the strip of tin-foil, with the window, I place as is shown in fig. 6. In my arrangement, the temperature of the strip of tin-foil rises in almost arithmetical proportion to the number of elements used,* when these are so arranged that each zinc is connected with a copper pole. With one element, and the arrangement just described, I obtain an elevation of temperature amounting to about 5° C. (9° Fahr.), and with six elements rather more than 30° C. (54° Fahr.). If great accuracy is required, the

* It must be expressly understood that the ratio here given corresponds only to a certain definite arrangement. It follows from Ohm's law that the resistance of the introduced strip governs this ratio. The strength of the battery required must be ascertained by experiment.

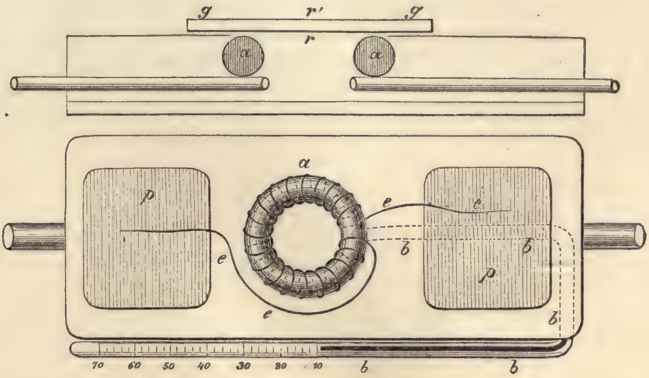
regulation of the temperature must be accomplished by means of a rheostat.

In order to exercise a direct control over the temperature of the glass cover, I attach a thermometer to the slide itself. In fig. 6, *a* represents

Fig. 6.

A II.

A I.



Gas chamber, with thermometer, capable of being heated by means of a constant current.

the flattened bulb of the thermometer, whilst the dotted line *b* indicates the direction of the tube. Both the tubes and the bulb lie in a groove made in an india-rubber slide. A coil of very fine copper or platinum wire is wound round the mercurial bulb *a*, and the ends are made to lie on the broad metal plate *pp*. The springs which conduct the current through the instrument press upon these plates.

Fig. 6. A II. is a longitudinal section of the stage in full working order; *g g* is the little glass cover, upon or to the under surface of which the object to be examined is attached. The cover is in contact, not only with the surface of the slide, but also with the coil of wire surrounding the bulb of the thermometer, the transverse section of which is seen at *a a*. When the circuit is closed, the wire becomes heated, and acts on the one hand upon the mercury, and on the other upon the cover. The hard caoutchouc is a bad conductor of heat, and hence the cover receives the greater part of the heat. The figure renders it apparent, also, how the slide can be at the same time used as a gas chamber.

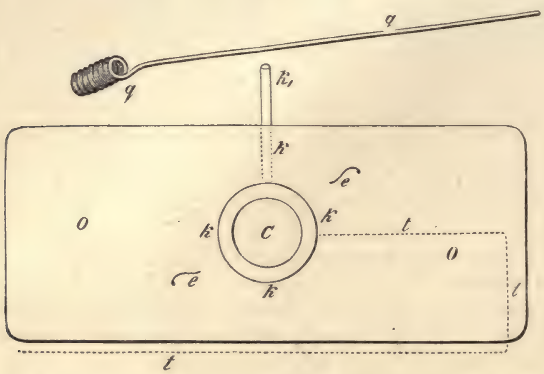
Where only the centre of the slide, or the cover, is desired to be heated, the flame of a candle or gas jet may be conveniently employed as a source of heat.

For this purpose a copper ring and rod of the form *k k k k* fig. 7 are so inserted into the glass slide *o o*, that they do not project beyond its surface; when it is required to be heated, the rod *q*, with its coil, is slipped over the free end K K, and to the extremity *q* the flame, which should be as small as possible, is applied. If the rod is of about the thickness of a large knitting-needle, it can be made of sufficient length to obviate any inconvenience to the observer from the flame. The centre C of the slide must be accurately arranged for a particular object glass, flame and focus. If a very small one be employed, we may reckon upon tolerable uniformity of temperature being maintained, though of course this mode has no pretensions to scientific accuracy. If, however, the general effect of an increase

of temperature within certain limits is all that is required, it is sufficiently useful. The facility with which it can be made renders it valuable for large laboratories.

I have constructed another slide with a thermometer attached, on the same principle of heating. The thermometer is fashioned, as in fig. 6, in the form of an arch, and is imbedded in a plate of caoutchouc. The bulb, however, is not surrounded by a spiral, but by a metal shell, which resembles *k k k* in fig. 7, and to this the projecting rod *k'* is fastened. If the apparatus represented in fig. 7 is imagined to be made of ebonite, and perforated in the centre, the dotted line will represent the position of the tube of the thermometer. Inasmuch as the object must in every case be placed on a covering glass, two clips (*e e*, fig. 7) are added to fix the glass. If

Fig. 7.



Slide capable of being heated, represented of natural size. *k k k k*, copper ring and rim imbedded in the plate *o o*; *q q*, heating rod; *e e*, clips.

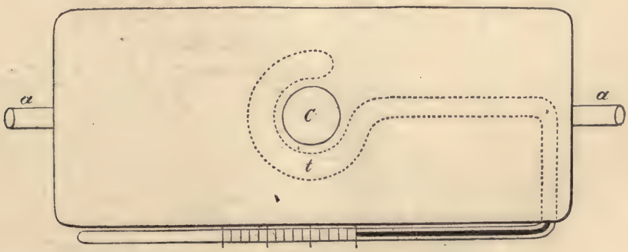
the plate is to be used as a gas cell capable of being heated, the object must be placed on the lower surface of the cover; but if only as a slide capable of being heated, it must be placed on the upper surface, and requires then its own cover. In the latter case the lower cover (*g g*, fig. 6. A II.) is equivalent to the ordinary slide, and only possesses the advantage of being a thin plate, the temperature of which can be easily raised.* The disadvantages of an ordinary gas cell appear prominently in the cell capable of being heated. In no arrangement with which we are at present acquainted does an equipoise between the preparation and the atmosphere surrounding it occur. The temperature of each part of the cover changes as the object glass sweeps over it, and must necessarily vary within certain limits, even with the best means of regulating the temperature. Each time that it is cooled, a precipitation of the watery vapor from the atmosphere that is saturated with it must occur. Recklinghausen and Kühne have endeavored to obviate this inconvenience by the construction of a more complicated apparatus for supplying heat. Whilst the results of these experiments are still unknown, it is advisable to postpone the investigations on the effects of heat in the gas cells. The reason that has induced me to describe the

* The mechanician, Heinitz, in Vienna, has constructed a gas cell capable of being heated on the model of that just described, with a degree of elegance that leaves scarcely anything to be desired.

construction of the heatable gas cell at so great a length is, that it affords excellent results in quite another line of inquiry. If the floor of the cell be covered with a drop of water, and the preparation is attached to the under surface of the cover over the water, all increase of temperature will cause the atmosphere within the cell to contain more watery vapor, of which a part will condense on the object. If a delicate test object be examined, such, for example, as the blood corpuscles constitute for a practised observer, it will be remarked that every addition to the temperature produces a perceptible alteration in the object, attributable to the increased proportion of water in the serum. We thus possess the power of supplying water, in very precise proportions, to preparations enclosed within a cell.

It has been further ascertained that the action of gases on blood is different in accordance with the amount of water that it contains. The results of the experiments that have been hitherto made will be detailed in the chapter on the blood. A single example may, however, here be given, to show the advantage that gas cells capable of being heated can afford. It may, in some cases, be very desirable to be able to vary the temperature within certain limits with rapidity. I have, indeed, had occasion to perform some experiments in which it was requisite to pass, alternately, iced water and steam through the cell. For this purpose I have constructed a metal slide, in which a central perforation (C, fig. 8) permits the passage of light; and the preparation may again either be placed upon a glass cover cemented down, or may be so arranged that the hole in the slide serves as a cell. The plate itself must consist of two leaves, so separated as to allow an evenly closed space to exist between them. Then, at opposite points of the space, two small tubes are inserted (*a*, fig. 9). To one of these an india-rubber tube *b* is attached, which leads to the vessel for generating steam F. This consists of a flask, through the cork of which a rectangularly bent glass tube is transmitted. The free end of this tube must now be brought into connection with the slide; in this communication a T-shaped tube is again introduced. A lamp with a small flame is placed beneath the flask,

Fig. 8.



Metal slide for the conduction of water and steam. *a a*, conducting tubes; *t*, thermometer.

which is half filled with water, so as to keep up gentle ebullition. The steam escapes through the perpendicular limb of the T-shaped tube, because it here meets with the least resistance. When, however, this is prevented, which is easily accomplished by means of a caoutchouc tube and a clip, the steam passes through the slide, and heats it. If the lamp is now removed, the cooling flask exerts a suction power on the vapor in the space between

the two leaves of the slide, and atmospheric air consequently enters; or if a receiver containing iced water be already prepared, this also may be sucked up, and rapid cooling effected. The temperature is ascertained by the thermometer, which occupies the position shown in the figure.

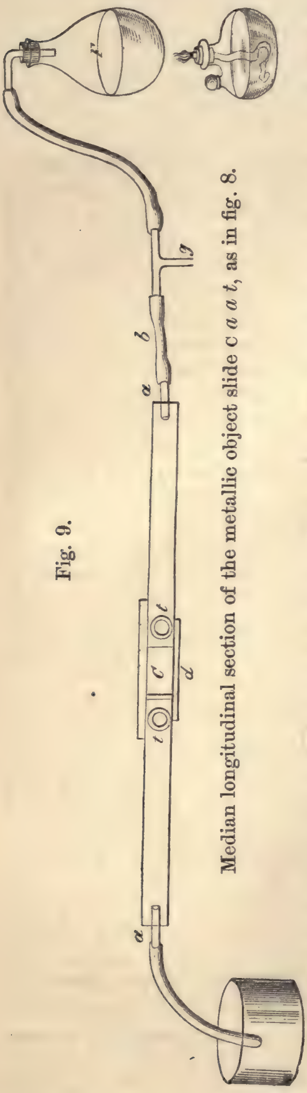


Fig. 9.

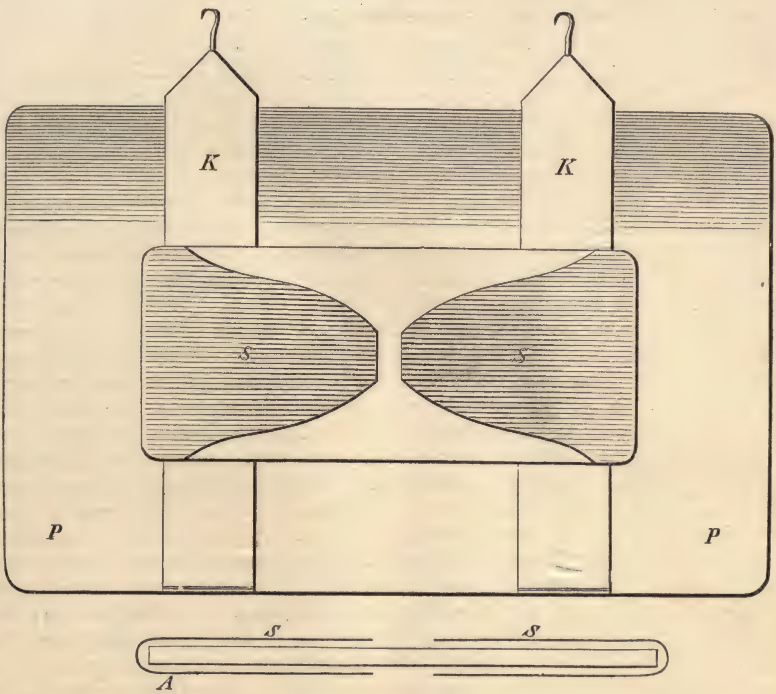
Median longitudinal section of the metallic object slide *c a a t*, as in fig. 8.

Electricity is also an agent of considerable importance in microscopical investigations. Brücke, in his physiological inquiry into the tissues, employed a slide covered with tin-foil, as shown in fig. 10. The slide S S was placed on two copper supports K, which were attached to the stage P. The electrodes were fastened to the supports, and the object was brought between the points of the lamina of tin-foil. The mode already described of obtaining and transmitting a current for the purpose of observing the effects of heat, will also, of course, serve for observing those of electricity. When this is the object in view, the slide should only be covered on its surface with tin-foil, in the form represented in fig. 10. The springs resting on ebonite rods will serve as conductors. The distance of the laminæ of tin-foil from one another is of importance in regard to the transmission of the current. As a general rule they should not be separated from one another to a greater extent than a few millimetres. I prefer to see the two electrodes at the sides of the field, because then the position of the object in regard to them, and to the middle line, is simultaneously visible. It is a matter of very great moment to observe and distinguish between the effects of the current in the immediate neighborhood of the poles, and at some distance from them; for the effects of electrolysis are produced on breaking the current in the vicinity of the electrodes, and the tissues become altered as they would be were they subjected to the action of weak acids or alkalies.

At parts more remote from the electrodes changes also occur, which, however, are not so remarkable as those which are induced by the chemical processes above alluded to. The effects which may be trusted as being really due to electricity should occur quickly after the passage of the current, and not be limited to the part in the immediate neighborhood of the electrodes. If the current be allowed to pass for some time, that is to say, for more than a few seconds, through the tissue, the products of electrolysis first extend over the whole surface lying between the electrodes, and then the intensity of the current becomes extraordinarily reduced, frequently, indeed, to zero, on account of the pole becoming covered with bubbles of gas. On this account the employment of constant currents for microscopic investigation is scarcely to be recommended, for with the closure

of even very weak currents, so violent a development of gas occurs, that but little confidence can be placed in the results that are observed to follow their passage. The amount of electrolysis that occurs with induction currents is much smaller, and they have therefore been most generally em-

Fig. 10.



ployed. The arrangement in which there is a single shock on opening and closure of the current is particularly advantageous. The shocks obtained from a Leyden jar are infinitely superior to the constant currents, because the instantaneity of the shock causes the disturbing influence of the evolution of gas bubbles to be altogether abolished.

It is not practicable to carry out the examination of tissues, under the influence of electrical currents, with the same elegance of detail as can be accomplished when a simple slide only is employed. The single circumstance that the tin-foil, in adhering to the glass, makes the surface irregular and uneven, renders it necessary that the sections of the preparation should be thicker, and proportionately interferes with the investigation by means of high powers. I endeavor, therefore, to combine my researches with electrical currents, with those conducted in the gas cell. By this means I am able to avoid the inconvenience alluded to: for if the cavity of a slide, adapted as described above for a gas cell, be surrounded by a layer of soft cement, it is quite possible to place the electrodes in close proximity with the preparation which is on the inner side of the cover, and to examine it in consequence with high powers. I attach to each side of the slide a strip of tin-foil, which passes over the putty, and reaches its inner side (*s s*, fig. 11).

Cemented to the cover are also two small strips of tin-foil (fig. 11, $s' \, s'$), which, running in the axis of the cover, leave between them a space of a few millimetres in diameter. The object is placed at this spot, and the cover is so disposed on the wall of putty that the metallic strips of the cover lie

Fig. 11.

on the strips covering the putty, and the cover is then firmly pressed down on the soft putty. The cell being now complete, the electric current is conducted by the strips of metal to the object, through which it passes at the same time; this lies immediately beneath the cover, and can, therefore, be examined with the highest powers. It is, moreover, no small advantage to combine the application of electricity with researches on the influence of gas, because we can neutralize or aid the effects of the current by the introduction of different gases.

On breaking the current, heat is developed in the tissue. I have measured the amount thus set free in my arrangement of the induction current, and find that it amounts, when the core is fully thrust down, to about 3° C. ($5\frac{2}{5}$° Fahr.). If an uncovered drop of blood is under examination with strong ordinary lenses, these become dimmed at the instant of the passage of the current, but after a short period they again become clear. The preparation, however, very soon dries up. It is requisite in such cases to determine what are the effects of the sudden elevation of temperature, and what are those of the electric current alone. An additional means of research consists in effecting a change in the fluid components of a microscopic object. We have not as yet been able to succeed in combining this mode of investigation with the application of gases. A reliable experiment in which an alteration in the fluid is effected is only practicable when the object is placed between the slide and the cover, the borders of which at two opposite points at least have not been oiled. To one of these points a strip of filtering paper with sharply cut edges should be attached, and at the other the fluid which is to be applied may be introduced by a small tube, one end of which has been drawn out into a long point. When the strip of filtering paper is attached to the side of the cover, it sucks up the fluid of the preparation: a current is immediately established, which as a general rule carries everything off that is not firmly adherent. If a little time is now allowed to elapse, it is possible by the cautious application of a very small strip to cause a slow and feeble current to pass over the superficies of the preparation whilst the deeper part remains at rest. If at any time the fluid is altogether withdrawn, the cover sinks until the deepest layers of the solid elements which cling to the cover are pressed flat, unless, indeed, they are too resistant to permit of such compression. As often, however, as a fresh drop is supplied from the other side, the cover again rises. In such experiments the focussing screw of the microscope must be deftly handled, if it be desired to keep the attention fixed on any given object. By the foregoing method a microscopic object can be washed in a chemical sense. Living morphological elements bear such an operation only so long as the fluid supplied is of an indifferent nature. The operation of washing can, however, be more freely performed in the case of dead tissues, to which, also, water and various re-agents can be alternately applied.

The formed elements may even be killed whilst under observation, and be then submitted to further reactions.

Water may be transmitted so as to allow it to be seen how young cells become spherical, and how a dancing movement of the granules in their interior occurs, how the nucleus becomes more clearly visible, and how they ultimately burst. On the application of acids, again the definition of the nucleus may be seen to become sharper, followed by the shrivelling of the nucleus, whilst the material which surrounds it loses its well-defined contour, becomes paler, and gradually disappears. Formed elements with hard outlines can be seen to swell up on the addition of alkaline solutions. Lastly, dissolved coloring matter may be introduced, and the gradual process of coloration of the formed elements or of certain constituents of the preparation may be witnessed.

Preparation of Tissues.—If the constituents of the tissue—that is to say, the formed elements—do not form a solid mass, but only a loose texture with larger or smaller interspaces between them, no special preparation is required for their examination. A small quantity is placed upon the slide, and covered with a plate of thin glass. If the formed elements are in too close juxtaposition, a drop of fluid may be added. It is to be borne in mind, however, that it is impossible to say of any fluid that it constitutes an indifferent medium for fresh tissues of all kinds. In all instances we must be prepared for changes taking place. Amongst those fluids which are most indifferent are, the fluid of the aqueous humor, the serum of blood, and amniotic fluid in which a little metallic iodine * has been dissolved—the so-called iodized serum; finally, very diluted solution of neutral salts may be particularly recommended. If the formed elements have been already modified in their chemical characters by the addition of other reagents, if, for example, they have been soaked in a dilute solution of bichromate of potash, or of chromic acid, water alone may be added. Reagents which induce coagulation of the formed elements, and a consequent hardening of the tissues, cause them also to become cloudy. In order to examine such changed elements with any advantage by means of transmitted light, it is customary to apply highly refractive fluids, which, when they penetrate into their interior, render them transparent. The employment of these means has led to very remarkable advances in microscopic art.

The highly refractive medium must be soluble in the fluid in which the tissues had previously been macerated. Glycerine is a highly refractive liquid of this nature, and it is soluble in water. Tissues can therefore be removed from watery solutions and immersed in glycerine, or what comes to the same thing, glycerine may be directly employed as a fluid for mounting microscopical preparations. Oil of turpentine is still more highly refractive, but it is insoluble in water. A tissue cannot therefore be removed from a watery solution into oil of turpentine. But alcohol is soluble both in oil of turpentine and in water. If, therefore, it be desired to impregnate a tissue with oil of turpentine, it is first removed from its watery solution into absolute alcohol, and from this into the turpentine. In cases where the tissue forms a membrane, it is only requisite to spread it out when fresh; to add a drop of some indifferent fluid, and then to cover it with a plate of thin glass. This plan, however, is only feasible when the membrane is not too thick.

* The amniotic fluid should be pure and almost destitute of smell. A trace of putrefaction renders it less available. The addition of iodine colors the fluid of a feeble yellow tint.

As a general rule, fresh tissues are more or less transparent, but after death they become cloudy. When, therefore, dead membranes are spread upon the slide, and are required to be examined with transmitted light, it is necessary, unless they are extremely thin, to add some highly refracting fluid. In the so-called parenchymatous organs—as the liver, spleen, and others—in the parts of the central nervous system, and in bones—nothing is usually to be seen, either in the fresh or in the hardened condition, so long as the connection of the morphological elements is not disturbed. It is requisite, in such instances, either to tease out small portions with needles, or to cut very thin sections.

a. The Preparation of Specimens by Teasing.—Specimens may be prepared in this way on the slide, a very small quantity of fluid being added: A minute fragment of the tissue should be placed on the drop, and then seized and torn by two sharp needles. Fibrous tissues can then be unravelled, as far as the vision of the observer and the optical means at his disposal will allow. The breaking up of tissues in this way is, however, accomplished, as a general rule, with less ease when fresh than after they have been macerated. The connecting substances which unite the formed elements are frequently of too firm a consistence to allow of their being thus torn, and the latter, therefore, are the first to yield, so that it is rare to see the formed elements whole and perfect. In such cases it is expedient to macerate the tissues for some time, in order to effect the solution of their connecting material. Solutions of potash have been applied, with this object in view, as well as of hydrochloric acid, bichromate of potash, Müller's fluid, and very recently, with excellent results, iodized serum. Lime or baryta-water is to be recommended for the isolation of the fibrils of connective tissue, whilst for the separation of the fibres of transversely striated muscles the tissue should be macerated in very dilute sulphuric acid, at a temperature of 40° C.; or it may be boiled in a mixture of chlorate of potash and hydrochloric acid. The most delicate manipulation of all is required for the isolation of nerve cells and their processes.

b. The Preparation of Specimens by Section.—It is only in some rare instances that sections can be made of animal tissues, either when fresh or after maceration, of sufficient delicacy to allow of examination with moderately high powers. Teeth, bone, and cartilage constitute, however, exceptions to this statement. Bone can, even when fresh, be cut into thin disks with saws, which may then be rubbed down with emery on a roughened glass plate, and polished on a hone. Cartilage requires no preparation, as thin sections may be readily cut from it with a sharp knife. The teeth are too brittle for the application of a saw. They should be attached to a cork by means of shellac, and rubbed down upon a whetstone. As a general rule, artificial methods of hardening the tissues must be employed. The simplest and most elegant mode is that of refrigeration. The tissue to be examined is placed in a little platinum capsule, and imbedded in the freezing mixture; then, as soon as it has become hard, sections may be made with a cold knife. A second method of hardening that is in constant use is that by means of alcohol. The tissue, divided into small pieces, is placed in a flask containing absolute alcohol, which is renewed every few days, according to the amount of water present in the object. For membranous tissues, boiling in vinegar was at one time adopted, but so many better plans are now known, that it has with good reason fallen into disuse. If it be desired to harden the tissues by boiling, the best fluid is one which

consists of eight parts of water, one part of creosote, and one part of vinegar; in this the tissues should be allowed to boil for two or three minutes, and be then laid out to dry. After two, or at most three, days it acquires a consistence which is admirably adapted for permitting sections to be made. The thin sections should then be treated with a little dilute acetic acid, in which the tissues again increase in volume, and they can then be examined either in water or in glycerine. If boiled preparations remain for a long time uncut, they gradually acquire such consistence that they are no longer appropriate for obtaining sections. This inconvenience has led to the method of drying. It is, indeed, much more advantageous to dry fragments of tissue. It is to be remembered, however, that the morphological elements of the tissues, in all these modes of hardening, are not so perfectly preserved as when they are kept in fluids. A means of hardening, of very general value and application, is found in chromic acid. This should be applied in solution, containing 0·25 to 2 per cent., and the perfectly fresh tissue ought to be placed in a large volume of the acid solution. The skin and all mucous membranes, the intestines, bladder, and conjunctiva, become in the course of a few days sufficiently hard to permit sections to be made; and even this period can be shortened by removing the preparation from the chromic acid solution, and immersing it in alcohol, where it may remain for twenty-four hours. The proper hardening of the brain and spinal cord, however, requires a longer time. Large portions generally putrefy in the centre, though they harden at the surface. These parts of the nervous system should therefore be cut into small fragments. Here also the subsequent application of alcohol proves of great service. The bichromate of potash acts in the same way as chromic acid, but much more slowly, the effect produced in a few days by the latter requiring weeks with the former. At the same time, the bichromate of potash possesses the very great advantage that the tissues saturated with it do not become friable. Recently, perosmic acid and chloride of palladium have been recommended as means of hardening, the solution containing from one-fifth to one-tenth per cent.

Various forms of apparatus have been constructed, by means of which fine sections can be made. It would be undoubtedly a great step in advance, if they could be made in any way which would render us independent of manual dexterity. But up to the present time these mechanical means have not attained sufficient excellence to lead to their general adoption. Sections are therefore still always made by the hand, and their beauty depends on the greater or less skill of the operator. The knives employed should always be of the best quality, and extremely sharp; scalpels will be found to be best adapted for objects that have been hardened by boiling, whilst large flat blades are more appropriate for those that have been hardened in fluids. The sections, when made, may either be examined without further addition; or they may be first prepared by means of needles, or be freed from adhering or imbedded morphological elements by the frequent use of a soft brush, or by blows with a delicate rod, or by shaking them in small test tubes. If the tissues are friable, or too small to be seized by the fingers, or possess a cavernous structure which it is desirable to preserve, or if they present irregularities and projections of the surface, like villous processes, or papillæ, and sections of these are required, the best method of dealing with the specimen is to imbed it.

The process of imbedding consists in dipping the tissue into some liquid which will easily set, even at the ordinary temperature of the air. For this purpose we may employ, first, a mixture of wax and oil, and secondly, a concentrated solution of gum. The first is prepared by melting oil and

wax, in equal proportions, in a porcelain capsule, by the heat of a lamp. The proportions of the two substances can, of course, be varied; and, according to the peculiarities of the case, whether it is required to be a little harder or softer, more wax or more oil must be added. The piece of tissue which is to be imbedded should first be kept in alcohol for a length of time sufficient to cause it to be thoroughly impregnated with that fluid, or, perhaps more correctly speaking, till the water it contains is as far as possible removed. This will occupy a longer or shorter period, in proportion to the strength of the alcohol; with absolute alcohol, and with small pieces of tissue, a few minutes are sufficient. The specimen is then to be placed in pure oil of cloves, which is far preferable to the oil of turpentine, that at one time was so generally used, partly on account of its more agreeable smell, partly because it is not so volatile, and partly also because it produces a consistence in the preparation more favorable to the obtainment of firm sections. The specimen must remain in the oil of cloves till it is transparent, the infiltration of the oil being incomplete so long as any opaque spots remain visible. A little cone of paper may then be prepared, which is to be filled with the mixture, and into this the specimen is placed, whilst it is still fluid. Before the mass cools, the position of the object should be noticed; and when it has become firm and opaque, its situation may be indicated by a mark on the surface of the wax, through which, when perfectly cold and hard, the section can be carried. The section must be floated off from the knife. Imbedding is best adapted for very delicate objects, which have little consistency, and which cannot well be seized with forceps or needles. A portion of the wax will always be removed with the section, and this must be detached from the knife by the aid of a little turpentine; the preparation will then float off, and may be placed upon the slide, or in a little cell, without further trouble.

If the preparation is to be subjected to no further manipulation, it is floated on to the centre of a slide, the superabundant fluid removed with care, and a drop of Canada balsam applied, after which a cover is placed upon it. The preparation is by this means completely preserved, and can be kept in this state and fit for examination for years. The process of imbedding in gum requires greater attention to minutiæ; but it is appropriate for specimens which contain much connective tissue, and answers for them much better than imbedding in wax. The preparation need not be impregnated with oil. It may be macerated for twenty-four hours in alcohol, of ordinary strength, and from thence be removed into a paper cone filled with a very concentrated solution of gum; the whole cone must then be immersed again in alcohol. In the course of two or three days the gum acquires a consistence which renders it very fit for making sections. No definite statement can be made in regard to the degree of this consistence, since it must be proportionate to the hardness of the tissue. Better sections are made of very soft tissues when they are imbedded in a mass which is not too hard, and *vice versâ*. The sections may be floated off by means of a little water, and be examined after the addition of a drop of glycerine; or they may be subjected to further manipulation. In the former case, if it be desired to preserve the preparation permanently, the excess of glycerine is to be removed from the edges of the cover, and these may then be painted with a layer of varnish, which hardens on exposure to the air. For this purpose a solution of asphalt in turpentine, the so-called asphalt varnish, or some similar material, may be employed. The preservation of preparations in glycerine exerts no prejudicial influence upon them, and when it can be used it is preferable to Canada balsam. Sections which have been taken out of

water may, however, be placed in alcohol, then in oil of cloves, and from thence they may be removed to Canada balsam, in which they may be preserved.

The contours of morphological elements, not previously visible, can often be made evident by treating the preparation with certain coloring matters. The principle of this means of research consists in the circumstance that various constituents of the tissues become quickly stained with coloring matters, or combine with them, whilst others do not. The tissues should be dipped in the solutions of the coloring agents, allowed to remain in them for some time, and then washed. *Cæteris paribus*, the concentration of the solution stands in inverse relation to the length of time required in order that certain effects should be produced. It is therefore advantageous to use very dilute solutions, and to prolong the time of their action. The more gradual this is, the more scope is afforded for exact researches.

A division of the coloring reagents can be made—first, into those, the solutions of which, when examined by transmitted light, show the same absorption colors they impart to the tissues; secondly, into those which impart to the tissue one of their own proper absorption colors; and lastly, into those whose solutions absorb no definite color, or are, as we are accustomed to say, colorless.

In the two last-mentioned cases, after saturation with the fluid, some chemical process must take place. An example of the first kind is seen in carmine, the alkaline solutions of which impart their own color to the tissues; an example of the second kind is met with in chloride of gold, the solutions of which are pale yellow, whilst the tissues that are saturated with it assume a violet tint; and an example of the third kind is found in nitrate of silver, the solutions of which are colorless, but yet stain the tissues of a dark brown hue. The secondary chemical change may either occur without further addition, or some means must be employed to induce it. When the tissues are macerated in dilute solutions of perosmic acid, they assume, sooner or later, according to their chemical nature, a black color, without any addition; but those which have been in solutions of nitrate of silver require exposure to light before the chemical change, which consists in the precipitation of silver, will occur. Gerlach introduced the method of examination by staining the preparation into practice. His first experiments were made with carmine. At the present time, however, many coloring agents are employed; specimens may be stained with tincture of saffron, with anilin, with indigo-carmine, hæmatoxylin, and picric acid; and also with nitrate of silver, chloride of gold, chloride of palladium, and perosmic acid.

When fresh membranes are to be acted on by nitrate of silver or chloride of gold, the pieces should be cut from the living animal, and thrown into the solution without further preparation. The solution should be kept in a dark place as long as the action is allowed to proceed; the preparation should then be recovered by means of sharp-pointed glass rods, washed, and placed in the light.

After fragments of tissue are taken out of solutions of silver, they may be placed in alcohol or glycerine, and then exposed to light; or the specimen may be prepared for microscopic examination in glycerine, and allowed to remain in it for twenty-four hours. Preparations which have been in solution of chloride of gold, after having been thoroughly impregnated with it, should be placed in water slightly acidulated with acetic acid.

If the action is required to be more intense, the membrane is to be well brushed, before it is removed from the staining fluid, with a wet brush. This is the best method of procedure, for example, with the centrum tendi-

neum of the rabbit, which should be thus brushed both on the abdominal and on the thoracic surface, whilst the cornea need only be brushed on the anterior surface, and then removed from the liquid.

In non-membranous tissues, just as in those which require to be broken or cut up for microscopical examination, the prepared specimen may be tinted whilst on the slide, after which it may be washed, and then covered in the usual manner.

Solutions of coloring matters which only act on the fresh tissues, as, for example, nitrate of silver, can obviously only be applied to sections made from recent and therefore necessarily frozen tissues. On the other hand, coloring agents which, like carmine, do not affect the fresh tissues, can only be applied to sections which have been made from dried specimens, or from those which have been hardened by chemical reagents. The particular mode of treatment adapted to each tissue will be described in the several chapters devoted to the consideration of each. The results obtained depend very much on the measures adopted, though it was thought it would prove of advantage to give here a general account of them.

Besides the mode of staining the tissues effected by dipping them in various solutions, another may be mentioned in which colored fluids are injected into the vessels. Formerly injections were only made with the object of rendering the lymph or blood-vessels visible by means of colored material, and the structure of the vascular walls was wholly disregarded; but in the present day injections are made with the object of exhibiting the structure of the parietes of the vessels. For this purpose, for example, a solution of nitrate of silver may be injected. Where, however, a solution of this kind is employed, the tube which is introduced into the vessel, and termed the canula, must be made of glass or platinum, and be connected with the syringe, which should be constructed of the same material, by means of an india-rubber tube.

Instead of the syringe, an apparatus may be applied in which the injection fluid is propelled by the pressure of air. This mode of injecting, first introduced into practice by Ludwig, is far more certain and elegant than the old method of the syringe. The injection fluid is, once for all, placed in a Woulf's flask, the size of which is appropriate to the quantity of fluid required to be used. Into one neck of the flask a tube is inserted air-tight, and reaching to the bottom, the upper extremity of which is bent at a right angle, and drawn out into a point: the other neck of the flask is surmounted with a short and also rectangularly bent tube. When this is connected with an apparatus from which air can be driven under a definite pressure, the injecting fluid must be expelled from the opposite tube. If, now, a canula connected with a short india-rubber tube has been fastened into a blood-vessel, and has been subsequently filled with an indifferent fluid by means of a pointed glass tubule, the apparatus can be at once put into action; and when it is seen that the injecting fluid begins to be discharged at the pointed extremity of the tube connected with the Woulf's flask, that point is quickly introduced into the india-rubber tube of the canula, and the apparatus is allowed to work as long as the injection will last. The mercurial apparatus of Hering is well adapted for the expulsion of atmospheric air. If this is not to be obtained, I apply the jet of the waterpipe on the same principle. The atmospheric pressure of the apparatus is measured by means of a manometer, and the rapidity with which the injection is forced onward can be regulated by retarding or accelerating the entrance of the mercury or water.

When the blood-vessels are to be injected, the canula must in all instances

be introduced and fastened into the vessel; but, in the case of lymph-vessels, according to Ludwig, the canula need only be stuck into the tissue, and firmly tied to it.

The point of the canula should be cut like a pen, and there should be a groove behind the aperture to prevent the ligature from slipping. In the injection of blood-vessels, all means of escape should be stopped, with the exception of one; and when the fluid flows freely from that, no more fluid should be injected. The injecting fluid distributes itself gradually through all parts, if the pressure be steadily maintained. Even though it is discharged to some extent at one point, injections with solutions of silver should be kept up for at least half an hour, under very gentle pressure; and, in this case, it is not requisite to tie any vessels when the injection is completed. It is only requisite to throw the tissue into dilute alcohol, in order to preserve it perfectly. When it is only required to show the blood-vessels, and not the parietes of the vessels, colored fluids should be employed; and if the arteries and veins are to be distinguished, each system must be separately injected with a fluid, which must not traverse the capillaries. The material in which the coloring matter is suspended is usually wax, and the coloring substance some granular pigment, as vermilion, red lead, etc. The injection can only be satisfactorily made with a warm syringe and warm tissues, as otherwise it cools too rapidly. After an injection of this kind has been made, the structure of the tissues can no longer be investigated. We can only discern one or more layers formed by the ramification of the vessels, and of course the object can only be examined by direct light. Injections thus made are also used for the so-called corrosion preparations. In the production of these, the organ, after being injected, is immersed in some reagent which destroys the tissue, whilst it leaves the injected mass intact. The form of the vascular network is thus obtained in colored wax, and such preparations can be put up in various ways under glass and in frames. Injections made with transparent solutions are now very common. A canula is inserted into an artery, and the fluid allowed to discharge itself by a vein. The dissolved material penetrates the capillaries whilst the coarsely granular pigment is stopped in the larger vessels. In such preparations it is obvious that no difference can be seen between the arteries and the veins; but, in this condition, they are not fit for microscopic examination. It is still requisite to harden them by freezing mixtures, or by means of alcohol, and then to make fine sections. In these injections it is always requisite that a certain fulness and tension should be given to the vessels; their forms then assume greater definition, and are generally more similar to their natural condition. On this account it is advantageous to dissolve the coloring matter in something which will readily coagulate, and which consequently affords all the advantages of a hardened tissue. Fine gelatine is usually employed, and is dissolved in water over a water bath, the coloring matter already in solution being then added, and the warm mass introduced into a Woulf's bottle, which again must be immersed in a warm water bath. The injection with gelatine is sufficiently tedious if required to be done thoroughly, as the mass stiffens too easily. The organ to be injected should therefore be brought into a warm room, and, where practicable, placed over a water bath which is adjacent to the former one.

The coloring matters usually employed are Prussian blue and carmine; the latter not in a state of complete solution, but partly precipitated by the addition of a little weak acid from its alkaline solution. Thiersch, whose transparent injections are perfect models of this kind of art, uses a transparent green and yellow. He obtains the former from chromate of potash

and nitrate of lead, the latter from a mixture of this with blue. When the injection with gelatine is completed, the open vessels must be tied, and the organ introduced or suspended in alcohol contained in a wide-necked bottle, pressure being carefully avoided. In order to obviate the inconveniences of the method of injecting with warm fluids, Beale recommends a fluid that can be used cold, consisting of coloring matter, water, glycerine, and traces of hydrochloric acid. When the organ has been injected, it is placed in absolute alcohol, and then treated as before. This mode of injection is very convenient, the vessels acquiring a very pretty color; but they can only be used on organs possessing a certain consistence.

Lastly, the method of self-injection occupies an important position amongst the various modes of injection. It has long been practised in the case of the vascular system of the frog. A pointed glass tube, filled with the colored injecting fluid, is inserted into the vena cava, and distributed through the system by the force of the heart itself. Kühne and Chrzonszczewsky have just injected the biliary vessels of living animals by means of coloring matter introduced by the jugular vein. Toldt has very recently practised a similar method for injecting the lymphatics. In the case of the biliary ducts a coloring material (indigo-carmine) in solution is employed, in order that it may be transmitted through the liver cells into the ducts; but in the case of the lymphatics a granular pigment (anilin) precipitated by water from its alcoholic solution, is introduced into the blood. Connected with the introduction of granular pigment is the method of coloring organs through the agency of the food, which has of late years assumed so much importance. This subject will be treated of at length in the first chapter of this work.

CHAPTER I.

THE GENERAL CHARACTERS OF CELLS.

BY S. STRICKER.

INDEPENDENCE OF CELLS.—In the year 1835, Joh. Müller commenced an essay on *Organism and Life*,* with the following words of Kant: "The cause of the particular mode of existence of each part of a living body resides in the whole, while in dead masses each part contains this cause within itself."

From this quotation it is sufficiently evident what rôle was at that time ascribed to the microscopic constituents of the body from the point of view taken by biologists. Fibres, cells, spheroids, and granules were distinguished under the microscope, and it was stated that these structures were not independent so far as their growth was concerned, but were subject to the influence of the vessels. They were on this account differentiated from vegetable tissues, which were supposed to possess an independent existence. A few experiments, however, led to the establishment of certain analogies between vegetable and animal cells. Joh. Müller himself, for example, pointed out the analogy that obtains between the cells of the chorda dorsalis and vegetable cells; and subsequently, when Valentin discovered the nuclei of the cells of the epidermis, he commented upon their similarity to those of the cells of plants.

Henle† made a decided step in advance when he proved that the epidermis cells, as they become more superficial, increase in diameter. An instance was thus given of increase without the intermediation of vessels. Schwann‡ seized the various analogies and points of relation between the cells of animals and plants in a comprehensive and fundamental proposition. Animal cells, he said, are completely analogous to vegetable cells, and are quite as independent in their mode of growth. The vessels of the animal body only cause variations in the distribution of the nutritious fluid.

Joh. Müller § at once and unreservedly adopted this proposition. His observation, that the works of Schwann were the most remarkable that had hitherto appeared in the domain of histology, certainly greatly aided the rapid acceptance they everywhere obtained.

Virchow had already compared the whole organism to a free state, containing individuals endowed with equal privileges if not with equal powers. The views entertained of the physiological significance of the constituents of the tissues, and especially of the animal cells, became, in consequence, completely modified. An impulse leading to the further extension of these ideas resulted from the examination of the lower forms of animal life. Dujardin ‖ had discovered in the year 1835 a contractile substance capable of movement in the lower animals, to which he applied the name of sarcode.

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* *Physiologie*, Band i., 1835.
† *Symb. ad. Anat. vill. intest.* Berlin, 1837.
‡ *Mikroskopische Untersuchungen*, 1839.
§ *Jahresbericht*, 1839.
‖ *Annal. des Sci. Nat.*, Tom. vii.

The singularly interesting phenomena exhibited by the living sarcode has attracted the attention of many observers, as Meyen,* Huxley, Max Schultze, and Joh. Müller. It was regarded as limited to the lower animals; and though destitute of nerves, the possession of irritability was ascribed to it.† Meyen's attempt to show that the Infusoria were unicellular organisms was indeed refuted, but it was admitted that a little mass of sarcode constituted a living and independent being.

The discovery of Siebold,‡ that the vitelline spheres of the egg of the Planariæ exhibit alternate contractions and dilatations, which, under favorable conditions, continue for hours, and the various subsequent discoveries of similar movements, or changes of form occurring in the colorless blood corpuscles, in pigment cells, and elsewhere, have led Kölliker § to express the opinion that the contents of all cells are contractile.

Virchow ‖ gave a still more precise expression of opinion when he stated that ciliary movement is to be attributed to a contractile substance; to which conclusion he was drawn by the discovery that under certain circumstances these movements, after having ceased, could again be excited by dilute solutions of the fixed alkalies.

Leydig ¶ referred to the significance of the movements occurring in the spherules of the yolk, which he, in common with Ecker, regarded as evident phenomena of life.

Kühne ** undertook a series of comparative physiological and chemical researches on muscular substance and sarcode, and pointed out the similarity of the phenomena they presented in the act of dying.

By all of these, however, the sarcodal substance was regarded as something different from animalcules, and as a material *sui generis.*

Max Schultze †† was the first to show that sarcode is analogous to the body or contents of animal cells, and that on this account the infusorial animacules possessed of independent life were simple or compound (fused *inter se*) cells. Schwann's views received support from these statements. According to the new doctrine, the cell was the typical form element of nearly the whole organic kingdom. The previous inquiries on the contractile sarcode could now be applied to the knowledge of the animal cell, and the renewed parallel investigations between sarcode and the protoplasm of the plant on the one hand, and of animal cells on the other, undertaken by E. Brücke,‡‡ E. Häckel,§§ Max Schultze,‖‖ and W. Kühne,¶¶ have, in very short space of time, advanced our knowledge on these points to a greater extent than the investigations of the preceding twenty years.

Brücke, who regards the cells as elementary organisms, admirably expresses the ideas, the development of which has been lightly sketched in the following passage:—

"If we consider," he says, "how complicated the mechanical arrangements must be which lie at the root of the spontaneous movements of cells,

* See the general literature of this subject in E. Häckel, *Die Radiolarien*, 1862.
† See Max Schultze's *Organism d. Polythalamien*, 1854.
‡ *Froriep. Notizen*, No. 380, p. 85.
§ *Würzburg. Verhand.*, Band viii.
‖ Virchow's *Archiv*, Band v.
¶ *Handbuch der Histologie*, 1856.
** Müller's *Archiv*, 1859, p. 817.
†† Müller's *Archiv*, 1861, p. 17.
‡‡ *Elementar-Organismen*, *Wiener Sitzungsberichte*, 1861.
§§ *Loc. cit.*
‖‖ *Protoplasm der Rhizopoden.* Leipzig, 1863.
¶¶ *Protoplasma und die Contractilität.* Leipzig, 1864.

and if we consider further that up to the present time we have only paid attention with the microscope to obvious and perceptible movements, and that no regard has been paid to the arrangements, by virtue of which the little organism nourishes itself, increases in size, and begets its like, nor any to those means by which it displays its specific attributes; if we, I say, consider all this, we must necessarily recognize that we have to deal here with an organism, the complication of which, although, truly, not comparable with that of an animal, nor affording any good reason for believing that it is itself composed of innumerable small organisms, yet constitutes one to which we may fairly attribute the possession of a highly artificial structure, the essential architectural elements of which are, however, completely beyond our grasp."

Ideal Type of a Cell.—Johann Müller proved that the cells of the chorda dorsalis possessed proper walls. In similar cells from the frog, Schwann demonstrated the existence of a nucleus, and was by this discovery first led to perceive the analogy between the cells of animals and plants. Here, then, we have a cavity bounded by walls, in the interior of which is a nucleus.

Scarcely any structure is to be met with in the whole range of animal tissues which is more suggestive of comparison with that which the botanists call a cell. (See p. 28.)

All animal cells were at this time considered to be constructed on the same principle, being held to possess a cell wall, enclosing a cavity, in which were fluid contents and a nucleus; when the membrane was not visible, it was either supposed to have burst, or was admitted to be present. In the cells of the egg a membrane was recognized by Krause,* from the presence of a double contour line. This mode of proof was not, however, strongly supported. C. H. Schultz considered he was able to exhibit the membrane of the blood corpuscles by the action of water upon them, inasmuch as they swelled up in this fluid, and assumed a spherical form; he also believed the nucleus revolved in the interior of the sphere.

The corpuscles of pus and of mucus had, however, even in the eyes of Schwann, no distinctly demonstrable membrane; he regarded them as minute roundish masses, containing a nucleus, which might be termed cells, because this was the elementary form of all animal and vegetable cells.

In accordance with the general views of Schwann, respecting the analogy of animal and vegetable cells, the ideal type of a cell was constructed.

Individual and scattered opposition to this ideal type of a cell was ineffectual so long as the whole theory of Schwann was contested, as it was, for example, by Arnold.†

With sure footing, and still resting on Schwann's conclusions, Leydig also abandoned the scheme of cell construction already mentioned.‡ He maintained that the contents of the cell are of higher dignity than the membrane, and constitute the material basis for the sensible and irritable processes; and that the conception of a cell requires the presence of only a little mass of substance, enclosing a nucleus. The cell membrane is, in his view, only the hardened external layer of the cell substance.

Max Schultze was, however, the first who effectually directed the views of histologists away from the idea of the vesicular construction of cells. As

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* Müller's *Archiv*, 1837, p. 139.

† See his *Anatomie*, 1845, Band i., p. 144.

‡ *Loc. cit.*

has already been stated, Max Schultze had himself furnished a new definition of a cell, which constituted an extension of the theory of Schwann. Max Schultze also defined the cell to be a little clump of matter (protoplasm), with a nucleus. The importance of this definition, however, did not lie in the fact that the existence of a membrane in many cells was denied—that had been already more or less positively stated before Max Schultze. The essential point was, that the identity of the so-called cell contents with the primary animal substance, or sarcode, was clearly recognized.

Little advance had, indeed, been made in the way of establishing a basis of life; for nothing more was known of the processes which take place in the living substance, than of those that were carried on in vesicles—perhaps still less—for all the phenomena of diffusion were intelligible on the vesicular theory, whilst it was difficult now to account for them. Naturalists, however, were familiar with irritable independently existing animals, but not with the idea of an irritable and independent vesicle obtaining its food by the laws of diffusion. The conception of a living cell body, or elementary organism (Brücke), has been an exceedingly satisfactory one to biologists, on the same principle that it gives us a great degree of satisfaction to be able to attribute to some familiar circumstance a noise in our sleeping apartment, on the origin of which we have long speculated in vain.

Those membranes of the animal cell which did not exhibit a double contour, were compared by intelligent histologists, not with the cellulose investment, but with the primordial utricle of the cells of plants. Botanists* distinguished a cellulose investment in the cells of plants, within which is the protoplasm that includes the nucleus and the solid and fluid contents of the cell. The protoplasmic mass externally, where it comes into contact with the wall of cellulose, was supposed to be invested by a very thin membrane—the primordial utricle. But Pringsheim† has shown that such a primordial utricle does not exist, the protoplasm lying in apposition with the inner surface of the cell wall. The term protoplasm has already been brought into use by Remak for the contents of animal cells. Max Schultze proposed to apply the term to the living mass of the cell, and since then the word protoplasm has been very generally employed.

Max Schultze‡ takes the embryonal cell as the basis and starting-point of his definition. "The most important cells," he remarks, "those in which the fulness of cell life, the unlimited power of tissue formation, is most distinctly evident, are clearly the embryonal cells, which proceed from the division of the cells of the ovum. We may see in these the true archetype of a cell, and yet they only consist of a little mass of protoplasm and a nucleus. Both the nucleus and the protoplasm are products of the division of similar constituents of another cell. Such cells include a living force in their interior, essentially possessed by the protoplasm, although it is true that the nucleus likewise plays an important part, not hitherto known with sufficient accuracy. The protoplasm is no farther isolated from external objects than by the circumstance that it will not combine with the surrounding medium, and that it constitutes, with the nucleus, a single whole. A distinct membrane may, indeed, appear on the surface formed by the conversion of the outer layer of the protoplasm, but then it must be allowed to be an early indication of a retrograde process. A cell invested by such a membrane can no longer divide—that is a power possessed by the enclosed protoplasm alone. A cell with a membrane differentiated in its chemical char-

* H. v. Mohl, *Vermischte Schriften, Botan. Inhalts*, 1845.
† *Bau und Bildung d. Pflanzenzellen*, 1854.
‡ *Loc. cit.*, p. 8.

acters from the enclosed protoplasm, is like an encysted infusorial animalcule."

Brücke* goes a step farther in his definition of a cell, maintaining that no proof has been given that the nucleus is indispensable to our conception of it. He rests his statement essentially on the fact that cells are known to occur in the cryptogamia in which no nucleus is visible. "We have," he says, "no positive information, either respecting the origin or the function of the nucleus; even the constancy of its occurrence appears to be subject to certain limitations, especially if we consider the cells of cryptogams, and do not start with the presupposition that, even in those cases where no nucleus is visible, it must nevertheless be present." The opinion of Brücke undoubtedly gains in weight, the more carefully the subject is considered.

Max Schultze † has discovered a non-nucleated Amœba (*Amœba porrecta*) in the Adriatic; E. Häckel ‡ a larger non-nucleated Protista (*Protogenes primordialis*) in the Mediterranean; and lastly, Cienkowski § has described two non-nucleated monads, namely, Monas amyli and Protomonas amyli. Häckel states, in reference to his protista, that it propagates by division.

It is, moreover, a fact, first made known by V. Baer, that the germinal vesicle of the impregnated egg—that is, the nucleus of the ovum—vanishes, and that the further process of development commences with a new generation of nuclei. I must express, in regard to the egg of the frog, my entire concurrence with V. Baer in regard to the question at issue. I have undertaken a great number of comparative investigations between fertilized and unfertilized ova in the same mode as that employed by him, and have found a germinal vesicle in the latter as a rule, whilst in the former there is only a cavity left, or even a total absence of any trace of its existence. But the ova of the more highly organized animals pass, as is well known, through various stages or grades of development till they reach a state in which their life terminates, and these ascending stages of development may, without straining the point, be generally compared with the ascending grades of organization which characterize the existing world. It is therefore but a step to admit that the commencing stages of the process of development correspond to the lowest forms of animal life. The existence of the non-nucleated cryptogams and of the non-nucleated protista which are now known, speak strongly in favor of such an analogy.

But if we desire to be logical, if we do not desire to advance the statement that the non-nucleated bodies of the lower plants and animals and the fertilized ovum occupy an unique and isolated position which is not assumed by any other being in the whole scale of creation, we must exclude the nucleus as an unnecessary factor in the ideal type of an elementary organism. We must also in future apply the histological term cell to the morphological elements of the higher animals or to independent living organisms, even if we are unable to discover anything more in their structure than that they are little masses of animal sarcode or protoplasm. Nor will any essential change be made in our views even if it be hereafter proved that there are cases where the nucleus is not only present but plays an extraordinarily important rôle.

I‖ have shown that little masses of protoplasm, destitute of nuclei, and

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* *Die Elementar-Organismen*, pp. 18—22.

† *Organism der Polythalamien*, 1854.

‡ *Zeitschrift für wiss. Zool.*, 1865, Band xv.

§ Max Schultze's *Archiv*, 1865.

‖ *Ueber contractile Körper in der Milch*, "On the contractile bodies in Milk," *Wiener Sitzungsberichte*, 1866.

which might be presumed to be the remains of cells, may still present some of the phenomena of life. I also now know that in other places where many young cells are collected together, fragments or minute separated particles occur about the size of a nucleus, which, if they become attached to the slide, sometimes exhibit very lively movements, and this especially if the object plate be warmed to from 68° to 70° Fahr.

May we now, in consequence of our new definition, consider these little masses as cells? and shall we be justified in giving this name to all the minute particles which, when armed with instruments of still greater penetration, we may be able to perceive and find capable of spontaneous movements? In the present state of our knowledge we shall certainly reply in the negative. We shall continue to regard such minute masses as living or organized matter without reference to their size, so long as the optical means of research at our disposal do not permit us to make the observations necessary for a different statement.

We cannot, however, term these masses cells, any more than we can apply the name of the whole animal to the excised heart of a tortoise. In order that we should apply the term "cell" to such an isolated fragment of living substance, it is necessary that we should recognize the whole group of phenomena which are characteristic of an independent animal—an independent organism.

Physiological Peculiarities of Cells.—Contractile substance, or protoplasm, appears, when examined with the best microscopes, to be homogeneous, or destitute of structure. It rarely occurs, however, in a pure state; for small particles are usually imbedded in it, which have either been taken up from without, or have formed in the interior as a consequence of chemical processes. If the protoplasm contain many colored corpuscles, the cell is termed a pigment cell; if it contain fat molecules, a fat or granule cell. The presence of small colorless, dull, or shining granules is indicated by the term granular applied to the cell, and of such cells two kinds are distinguished—those that are coarsely and those that are finely granular.

When other kinds of material are contained in the cell, their presence is indicated by appropriate terms. It is thus usual to speak of starch-holding cells, and the like.

Since the researches of Häckel (see p. 34) have shown us that foreign matters can penetrate into the interior of the protoplasm, the origin of all such particles must be investigated. We must determine in every case whether a body which lies in the interior of the cell is the result of some chemical process in the interior of the protoplasm, or has been introduced from without. If particles of coloring matter are artificially caused to enter, as has been successfully accomplished by Recklinghausen, Max Schultze, Billroth, Cohnheim, and others; then the question as to whence the coloring matter proceeds is answered by the experiment itself. But it is more difficult to decide from whence those bodies that are found imbedded in cells proceed, which occur without the agency of the experimenter. The determination of this point may prove, however, of extraordinary importance. Since, for example, Preyer showed that portions of red corpuscles are eaten by the amœboid cells of the frog, we could not admit without much proof that the presence of red corpuscles in the interior of the white was due to the development of the former in the interior of the latter.

The consistence of protoplasm varies within moderately wide limits. It may, like a fluid, form drops, assuming, when in small quantities, a spherical form, or may extend itself upon the slide like a gelatinous body; or, lastly, it may contract up into a resistant ball.

Protoplasm may therefore be said to be fluid, or solid, or gelatinous. Its

states of aggregation are subject to constant change, and none of the ordinary terms employed for this purpose will be in all cases accurate.

Protoplasm is termed a living substance, and the application of this term is based upon its exhibiting the sum of those phenomena which we have learned by experience to be characteristic of living animals. These phenomena are active or spontaneous movement, nutrition and growth, and the capability of reproducing its like.

The movement of cells is easily to be seen. The changes of which it is the result take place in so short a space of time that they may be followed with the eye. The growth of the cell is a process of a slower nature, and cannot be directly observed; nor has any one, as yet, been able to place the cells under the microscope, under such favorable conditions as to witness their increase in size. We must therefore be led by analogy to the conclusion that this really takes place.

Various observations have been directly made on the nutrition of unicellular animals. It may be seen how they take up foreign bodies, and nutritious material, into their bodies, and some of the changes of the material introduced may be followed. It is difficult to observe the mode of nutrition that occurs in the cells of the compound animal body, because the nutritive materials are brought to them in the form of solution in the juices of the animal body. Moreover, the processes by which the dissolved substances penetrate the cells is concealed from our observation.

The act of reproduction depends on two separate processes; first, on the growth of the mother-cell, and secondly, on the detachment of the daughter-cell (birth). The latter alone is subject to direct observation, and usually this only is understood when reproduction is under consideration.

Phenomena of Movement in Cells.—We conclude that movement occurs in cells, either from certain movements of the granules that are imbedded in the protoplasm, or from the occurrence of certain changes in the form of the protoplasm itself. The movement of the granules in this case is a passive movement. The granules which have been introduced from without, as well as those which have developed in the interior, providing they are not too heavy, move as the result of the action of the forces we are about to consider.

The movement of the granules is either continuous or vibratory.

The continuous movement, again, presents two forms; first, a relatively slow progression, corresponding to and following the changes of form of the cell.

Engelmann* states particularly he has observed, in the corpuscles of the cornea, that they begin to move in order, from before, backwards, and refers to similar observations of Hofmeister on the Plasmodia of the Myxomycetæ.

Secondly, There is a swifter flowing movement that far exceeds the changes of form of the protoplasm in rapidity.

Max Schultze describes the movement of the granules in the threads of sarcode that the Foraminifera project through the apertures of the shell, as a gliding or streaming motion of granules imbedded in a sarcodal substance.† "As the passengers in a broad street swarm together, so do the granules in one of the broader threads make their way by one another, oftentimes stopping and hesitating, yet always pursuing a determinate direction, corresponding to the long axis of the thread. They frequently become stationary

* *Ueber die Hornhaut.* Leipzig, 1867.
† *Das Protoplasm d. Rhizopoden*, p. 11.

in the middle of their course, and then turn round; but the greater number pass to the extreme end of the thread, and then reverse the direction of their movement." It cannot be doubted that these continuous motions depend on vital processes in the cells. At all events, we are acquainted with no analogous phenomena in unorganized bodies.

The vibratory movement of the granules calls to mind the so-called molecular movement of Brown. It may be witnessed in the salivary corpuscles, and under certain conditions in the colorless blood corpuscles, pus corpuscles, and others. On this account it has been doubted whether these movements really depend on the vital properties of the protoplasm. Such movements, it may be observed, occur also in dead cells, as in the case of granules that have escaped from cells undergoing disintegration, which continue to move, provided that the medium they enter does not present any obstacle.

Similar movements, too, are found in cells that are clearly living. The dancing movement ceases in the interior of the corpuscles of saliva on the cautious addition of a solution of common salt, containing from $\frac{1}{2}$ to 1 per cent.; but this still permits the movements of fresh pus or lymph corpuscles to continue.

Recklinghausen* has described similar phenomena in the latter kind of corpuscles. When the menstruum is diluted with water, they become spherical (an experiment that had already been performed by H. Müller and Reinhardt),† and the granules in their interior begin to dance; but as soon as the fluid becomes somewhat more concentrated in consequence of evaporation from the margins of the cover, this vibratory movement ceases, and the corpuscles commence again to undergo their customary changes in form.

We see here, then, clearly enough, that two phenomena alternate: if the corpuscles are spherical, the granules dance in their interior; but if the corpuscles undergo changes of form, then the granules cease to vibrate. It is rare to see the so-called molecular movements in cells which change their shape. It may, however, be occasionally observed in the colorless blood corpuscles of the newt, after the addition of water. The question whether the vibratory movement of the granules stands in relation to the life of the protoplasm is only applicable to such living cells.

Brücke ‡ has referred to the possibility of this connection, in consideration of the circumstance that the movements are arrested by induction currents of sufficient intensity.

Böttcher,§ on the other hand, has expressed his doubt upon the existence of any such connection, on the ground that the granules which vibrate in the cells continue the same movement when they have escaped from the interior (by bursting of the cells), provided that the medium into which they pass is of an appropriate nature.

Neumann ‖ founded his objection on the fact that the vibratile movement still occurred in cells which were dead or on the point of death.

The idea of a connection existing between the movement and the life of the protoplasm is essentially based upon these facts; first, that the cells in which it occurs are living cells, and secondly, that changes in the phenomena of life induce, or are followed by, changes in the motion of the granules. In

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* Virchow's *Archiv*, Band xxviii.

† Virchow's *Archiv*, Band i.

‡ *Ueber die sogenannte Molecularen*, "On the so-called Molecules," *Wiener Sitzungsberichte*, 1862.

§ Virchow's *Archiv*, Band xxxv.

‖ Reichert and Du Bois Reymond's *Archiv*, 1867.

the mean time, observation of the movement of the granules alone cannot enable us to draw any conclusion in regard to its dependence on life, so long as it is only a vibratory and not a progressive movement, and so long as some peculiarities are not discovered in these vibratory movements, which justify such a conclusion.

a. CHANGES IN FORM of the entire mass of the protoplasmic mass are most strongly marked in the lower forms of animal life.

Max Schultze,* in his description of the mode in which the Amœba of Ehrenberg or Proteus (O. F. Müller) obtains its food, furnishes the following lively picture of its movements:—

When an Amœba approximates another animal whose movements are not so swift as to enable it to escape from its enemy, it embraces it with its many-stalked body. The processes meeting on either side, coalesce, and after thus investing the whole mass with animal substance, the Amœba maintains its grasp till it has abstracted all the portions that are soluble. On account of this remarkable peculiarity of the Amœba, those cells which possess the power of spontaneously moving, are termed amœboid cells. It is rare, however, for the cells of the more highly organized animals to move so rapidly as the Amœba itself.

Their movements are either limited to gradual change of form, or to the protrusion of processes which either drag the rest of the body after them, or are again withdrawn. The processes may assume the form of threads, swellings, tuberous elevations, or broad flattened projections or tufts, and may present the greatest diversities of form.

If the alterations in shape are desired to be accurately noted, the cell must be placed upon a slide, or on a piece of tissue, or may even be attached to the cover; for if the cells swim in fluid, it is possible they may turn, and thus present different surfaces to the observer. No conclusion can be drawn respecting the life of a cell, from the observation of a single change of form, since it is impossible to ascertain whether some unknown physical influence may not have wrought the change. Those alterations of form only which may be perceived in the object when the field of view is stationary, and when the object is adherent to the slide, and which are frequently repeated, enable us to determine the presence of life in it.

Conversely also, we must not consider a quiescent protoplasmic mass as necessarily dead, even if we are unable artificially to excite movement by means of reagents. The protoplasmic substance may possibly be encapsuled when it is not in a state to change its form, and even if it be naked, some unknown cause may hinder its movements. Hence, it cannot be said that the salivary corpuscles are dead, because as a rule they do not change their external form.

Protoplasmic corpuscles are not only able to change their form, but their place also; they can wander. This is accomplished by the protrusion of one portion of their mass, which drags the rest after it. If such alterations of form are repeated several times, and in the same direction, locomotion is effected.

It must not be overlooked that entire cells may exhibit vibratory movements in fluids obviously subject to the laws of the Brunonian molecular movements. The stellate blood corpuscles of mammals, for example, do so as a rule. Such vibratory movements are to be clearly distinguished from the migrations of cells. Cells can only move from place to place when rest-

* *Polythalamien*, 1854, p. 8.

ing on a firm basis. They may swim in fluids, owing to the agency of currents, but not through their own active movements.

The capability of moving from one place to another, possessed by the Amœba, has long been known. The migratory power of the Foraminifera, by means of the processes of their structureless substance protruded through the openings of their shell, has also been frequently observed. But Recklinghausen* was the first to notice that the cells in complex animal bodies can also perform movements of locomotion, and by his observation introduced a fact to our knowledge having a very wide and important bearing.

E. Häckel, whilst injecting Thetis fimbria with indigo, discovered that fine particles of coloring matter could penetrate into the interior of the blood corpuscles. The artificial introduction of coloring matters into cells is now termed giving them a supply of food. If, into the medium in which the cells are suspended (for example, blood plasma), a finely granular coloring matter be introduced, some of the particles of the latter are soon found to cleave to the surface of the cells, and to pass from thence into their interior.

By the aid of this mode of supplying food, Recklinghausen has furnished the important proof that pus corpuscles are not always generated where they are found. He has shown that pus corpuscles can migrate into the meshes even of a dead cornea, and has by this observation opened up a new path for every department of pathological inquiry. These also are matters of fact that exert no little influence on physiology generally. I † have myself shown that in the construction of the body of the embryo, the movement of masses of cells to form the rudiments of organs, depends on the migration of the embryonal cells within the ovum. Cohnheim ‡ has also very recently, by demonstrating that the colorless corpuscles can leave the vessels, and migrate, and that there may be a transplantation of living cells from one organ into another, and from one region of the body to another, furnished us with information, the importance of which cannot at present be estimated.

Hering § has endeavored to explain the passage both of colored and of colorless blood corpuscles through the walls of the vascular system, by comparing it with the filtratiôn of colloidal substances. But in whatever way the process may be explained, the fact remains that the white corpuscles leave the interior of the vascular system, and are thus enabled to traverse various regions of the body.

In stating that protoplasm is capable of active or vital movements, we have by no means admitted the existence of an immaterial force. Ed. Weber ‖ has expressed himself very decidedly upon this point, and at the present day the position he took up is still tenable. "According to my view," said Weber, "the movements of any living body are not dependent upon two kinds of force—namely, first upon forces which are exerted on this body by other bodies, and secondly upon forces which are exerted on this body by life; but there is only one kind of force on which the movements of all bodies depend—namely, the force which is exerted on it by other bodies." We name the movements of certain bodies "vital," in the sense that the forces which we then call into play are subject to certain other varying influences, and we denominate the apparatus and the processes of which these influences are the result, "organization" and "life."

It is customary also to call the vital movements of protoplasm spontaneous. But

* Virchow's *Archiv*, Band xxviii.
† *Wiener Sitzungsberichte*, 1864.
‡ Virchow's *Archiv*, Band xi.
§ *Wiener Sitzungsberichte*, 1868.
‖ Müller's *Archiv*, 1858.

this only shows that we are ignorant of the forces by which the movements are originated and sustained. We no longer term the movement of striated muscle spontaneous, because we know the external influences or stimuli through which it can be excited. And so also there can be no doubt that as soon as we have acquired a knowledge of all the external influences by which movements in protoplasm can be induced, we shall cease to term them spontaneous. Thus, in an analogous case, we say the production of heat by coal is immediately dependent on our placing it on the fire, *i.e.* on raising its temperature. Here the process of heating is the external influence or stimulus which induces a change in the molecular structure; and as a consequence of this molecular change, active force is set free, which becomes perceptible to us in the form of heat. The production of heat by carbon is an independent power, dependent on the very nature of its substance, but it is by no means a spontaneous power. The analogy, however, has only a one-sided value, since, if the coal is once burnt, it can generate no new active force; but the contractile substance is capable of restitution.

The movements of contractile substances may be altered, accelerated, retarded, or altogether stopped, by external influences (stimuli), which may vary greatly in kind and degree.

Amongst the known conditions that exert an influence on the movements of protoplasm, we may enumerate the variation of temperature. The oldest reference to this fact was made by Weber,* when he said the movement of cilia could be accelerated by warmth. Kühne† also remarked that the motions of amœbæ could be arrested by iced water, but that on raising the temperature they recommenced.

Since Max Schultze‡ has made the warming of the slide an important assistance in micro-physiological investigations, we have learnt that the locomotive cells of warm-blooded animals can maintain their movements for a long time, external to the organism, if kept at the ordinary temperature of the animal from which they have been taken. We are unable, however, to give any precise statements possessing general application, respecting the influence of temperature.

Still, as a general rule, an exaltation of a few degrees above the temperature at which the organisms customarily live, accelerates their movements, whilst a corresponding depression retards them. If the temperature exceed certain limits, however, their life is imperilled. The eggs of trout, for instance, undergo segmentation capitally in iced water, but in a warm room soon die.

The influence of temperature on the movement of cells is a point of particular interest in reference to their migration. Max Schultze § has demonstrated that the colorless corpuscles of human blood are capable of effecting a considerable amount of locomotion at a temperature of from 100° Fahr. to 104° Fahr. It is well known how great is the influence of particular temperatures on the development of the egg, and even if the movement of the cells is not the chief factor in this process, it certainly plays a very important part in it. We may readily conceive that an analogous influence must be exerted by any increase of temperature occurring in pathological processes.

A peculiar effect of temperature is described by Kühne,‖ as observable in the fresh-water amœba, which at 95° Fahr. assumes a spherical form.

Lastly, Peremeschko¶ states that the large cells at the bottom of the yolk cavity in the eggs of fowls, contract and dilate at a temperature of from 89.3° Fahr. to 93° Fahr.

* Canstatt's *Jahresbericht*, 1847, p. 59.
† *Das Protoplasm.* Leipzig, 1864.
‡ Schultze's *Archiv*, Band i.
§ *Loc. cit.*
‖ *Protoplasma*, 1864.
¶ *Wiener Sitzungsberichte*, 1868.

b. Mechanical Influences.—Kühne was the first to comment on the effects of indirect mechanical irritation, stating that after he had stimulated the margin of the cornea in a frog, he saw stellate corpuscles become fusiform.

I* have made a few experiments on the effects of direct mechanical irritation, and have observed that when blood diluted with a solution of common salt, containing one-half per cent., is placed under a cover, and this last, by the withdrawal of the fluid, is allowed to sink to such an extent that the white corpuscles are flattened out, they alter their shape with considerable vivacity, especially if they are allowed to remain in this position for some time. If now a drop of fluid is brought to the margin of the cover, this will again be raised from the slide in proportion to the quantity added. The flat corpuscles may now be observed to contract into small angular lumps, and after a short time to change from this into a moderately expanded form.

The compressed corpuscles here behave like the muscles of insects under the compressorium, which continue their movements for a time, even when the pressure upon them prevents any increase in thickness. It is evident from this experiment that protoplasm is an elastic body, since it contracts when the extending force is removed. The contraction, however, appears to correspond here with the elasticity of the irritated substance, because a shortening occurs which is not maintained. An additional argument in favor of this view is, that the experiment is more successful when it is tried a second or third time. The corpuscles then contract much more energetically than at first.

c. Electrical Stimuli.—The action of electric currents on protoplasm is very variable.

The excitation of amœboid movements by means of weak induction currents has, up to the present time, only been observed by Kühne in amœbæ, and by Golubew in certain white corpuscles of the blood of the frog.

Kühne† saw amœbæ assume a spheroidal form, when made to form part of a constant current; whilst, after exposure to an intermittent current, the stellate corpuscles of the cornea became fusiform, and then reassumed their original shape.

Golubew‡ states, from experiments made in Rollett's laboratory, that after being repeatedly irritated the cells become flattened, but even in that state exhibit changes of form. If stronger stimuli are applied to them in this condition, the disc-like mass again contracts and becomes spheroidal. He further observes that the fusiform colorless cells of the blood of the frog, which present no spontaneous movements, when moderately irritated, contract to spheroidal masses, but soon again revert to their original shape. I§ have observed contractions and dilatations to take place in embryonal capillary vessels after the action of induction currents.

Kühne‖ has observed the following law of contraction in the protoplasm of Actinophrys eichhornii during the action of a constant current :—

	Positive pole, or electrode entrance of current.	Negative pole, or electrode exit of current.
Closure	Contraction	0
Current passing	Tetanus	0
Opening	0	Contraction.

* *Wiener Sitzungsberichte*, 1867.
† *Loc. cit.*
‡ *Wiener Sitzungsberichte*, 1868.
§ *Wiener Sitzungsberichte*, 1866.
‖ *Loc. cit.*

After being exposed to the action of moderately strong induction currents, protoplasm assumes a spheroidal form. This observation was first made by Kühne in the amœba, and has since been corroborated by Neumann, in regard to the colorless corpuscles of human blood, and by Golubew in those of the frog. Kühne states that amœbæ which have become spherical from the action of induction currents, after a short time recommence their ordinary movements. Golubew makes the same remark, but observes that the movements of the colorless corpuscles of the frog are of a more undulatory character, though they send out, as usual, pointed processes.

According to Neumann and Golubew, when strongly irritated, the granules in the spherical cells exhibit vibratory or so-called molecular movements.

Brücke * saw salivary corpuscles burst under the influence of strong induction currents. Kühne witnessed a similar phenomenon in an amœba.

Kühne describes the spheroidal condition of the amœba, produced by stimuli, as a kind of tetanus, and considers that, in the state of maximum contraction, these animals assume a spherical form.

Hermann, however, suggests an essentially different explanation. It is possible, he remarks, that the excitation diminishes certain resisting forces which have previously prevented the cell from assuming a spherical form. The spherical form therefore, he thinks, may correspond either to the state of rest, or to the state of tetanus.

Kistiakowsky † has observed an acceleration of ciliary movement to be produced by the constant current.

Engelmann ‡ gives the following series of laws of this action:—

(*a*) Every variation in the intensity of the current, whether positive or negative, providing it be sudden, acts as an excitant.

(*b*) A single variation in the intensity of the current induces a series of alternate contractions and relaxations.

(*c*) A single excitation induces changes which may be divided into three stages: That of latent excitation (which with opening-induction shocks is scarcely perceptible, and is hence generally longer the weaker the shock); secondly, the stage of increasing energy (which also lasts longer in proportion to the feebleness of the shock); and, lastly, the stage of diminishing energy (which is so much the more rapid the weaker the shock).

(*d*) The closure of a constant current is a stronger stimulus than its opening.

(*e*) The direction in which the current traverses ciliated cells appears to have no influence on the amount of irritation exerted.

(*f*) The movement may be retarded by the application of a very strong electrical current, or may even be altogether stopped, the cell at the same time being destroyed. The same thing occurs on producing long-continued tetanization with strong alternate currents.

d. Nervous Excitation.—On this point only a single direct observation by Kühne can be adduced; namely, that the contraction of certain stellate cells in the cornea of the frog may be induced by excitation of the corneal nerves. Brücke § had long before furnished evidence in regard to this by referring to the very well-marked phenomena of contraction that are visible

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* *Ueber die sogenannte Molecular-Bewegung, loc. cit.*
† *Wiener Sitzungsberichte*, 1865.
‡ *Centralblatt*, 1868.
§ *Denkschriften der Wiener Akad.*, Band iv., p. 203.

in the pigment cells of the skin of the chameleon, and which can readily be excited reflectorially by irritation of the sensory nerves.

e. Chemical Stimuli.—Amongst these we may first mention the influence of water. Amœboid movements can be excited in the segmentation spheres of the egg of the frog by the addition of water: hyaline processes are thrust out, in the interior of which a streaming motion of granules can be discerned, so that the form of the cell undergoes a change. At other times the processes are again withdrawn, or undergo repeated alterations of form after they have remained protruded for a short period. Ecker* regarded these phenomena as indications of spontaneous movement, but I† have shown that the movements of these cells, when no water has been added, are of quite a different kind, and that the above occur only on the addition of that fluid.

The streaming movements of the granules contained in the pseudopodia of the marine rhizopods is also arrested by distilled water.‡ The greater number of amœboid cells become globular when exposed to the action of water, but after a few seconds a vibratory movement of the granules is observable, after which the cells generally burst; some, however, remain globular for a time, and then recommence their amœboid movements: this is particularly the case if, as has already been mentioned, they are moistened with a one-half per cent. solution of common salt.

The cells that assume a globular form on the addition of water, seem also to increase in size, from which it may be concluded that they imbibe some of the fluid.

The laws by which water or a solution of any substance is thus taken up are unknown. It seems probable, however, that diffusion plays a part in the process.

We may also conceive that the water which has penetrated into the interior of the contractile substances acts as a stimulus, because we are already acquainted with the similar action exerted by water on muscular tissue, and because electrical currents produce similar effects on the cells.

The statement made by Hermann, that the spherical condition assumed by the cells in water or other dilute medium is a state of rest, is certainly plausible. The circumstance that they will remain spherical for hours, without losing their vital properties, as may be seen in the case of the salivary corpuscles, is also in favor of it.

The coalescence of the spherical cells described by Brücke, Neumann, and Golubew, can then be very naturally explained; for it may be said that, as a consequence of the stimulus, the opposing influences are diminished, and the protoplasm now follows the laws of ordinary liquids—it forms drops, and these coalesce. The act of bursting in water must, then, be regarded as due to a suddenly produced partial coagulation resulting from the more energetic action of the fluid.

If to the medium in which the spherical cells are contained a one-half per cent. solution of common salt is gradually added, the protoplasm resumes its apparent activity, and recommences the usual changes of form. But if the solution added be concentrated, the cells shrink up. It has not been, as yet, accurately ascertained what strength of solution is compatible with the life of the cells, nor for what length of time the action may be continued. The proportion of water in many protoplasmic substances may undergo great

* *Icones Physiol.*

† *Ueber die selbstständige Bewegung*, *Wiener Sitzungsberichte*, 1864.

‡ Max Schultze's *Archiv*, Band ii.

variations without destruction of life. The myxomycetæ can even be completely dried up, and yet when again moistened may continue to live.

Max Schultze and Kühne have observed similar results to those above described, to result from the action of water after the addition of very dilute acids and alkalies.

An elegant experiment has been made by Kühne,* showing the influence of gases on the movements of protoplasm. He has pointed out that the ciliated cells of the gills of Anodonta cease to lash in hydrogen and in carbonic acid, but that it is only requisite to admit atmospheric air in order to effect the re-establishment of the movements. This experiment shows that carbonic acid acts injuriously like other acids.

Weak alkaline reaction in the fluid in which the cells are contained, is favorable to their movements, but acids tend to arrest them.

The contractility of the protoplasm is of the greatest importance to the entire organism to which it belongs, for ciliary movement depends upon it.

As we now know from the researches of Schweigger-Seidel and La Valette, that the spermatozoids are not essentially nuclear structures, but are also composed of protoplasm, their movements must likewise be attributed to this substance.

Cell division and germination are likewise consequences of its contractility.

Lastly, also the migrations of cells are dependent upon it, of the importance of which to the organism at large we have already spoken.

Hermann has made an attempt to explain the phenomena of movement. The protrusion of a process, he says, can only be regarded in the light of a partial contraction, which, whilst it occurs in the direction of a striving on the part of the cell (or, better, of a striving surface), drives the superjacent segment before it. If, then, renewed contraction continually occur, it must always become thinner and more thread-like. Hermann makes no remark, however, on the retraction of the processes. But if Hermann's theory were adopted, there would not be much difficulty in explaining this by admitting contractions in other directions.

METAMORPHOSIS OF TISSUE.—Only a single direct observation by Kühne * exists in regard to the metamorphosis of tissue that takes place in the living cell. According to his researches, ciliary movement is connected with the consumption of oxygen, and there can be no doubt that the cells are capable of withdrawing oxygen from loose chemical combination. Ciliary movement continues in an atmosphere of hydrogen, and in a solution of oxygenated hœmoglobin, till all the loosely combined oxygen of the latter, as may be proved by spectrum analysis, is consumed. Moreover, from indirect experiments, we are justified in admitting a metamorphosis of tissue in the cells, and are hence in a position to realize the more accurate data which have been acquired respecting the metamorphosis of tissue in animals. The results which have been arrived at from investigation on muscles are particularly important. Muscular fibres are metamorphosed cells, and they consist essentially of contractile substances, the internal structure of which differs entirely from that of contractile protoplasm. But the muscular fibres are collected into great masses, permitting macroscopic investigations of a chemical and physical nature to be undertaken upon them which are not applicable to microscopic inquiries. The range and variety of experiments performed under the microscope is undoubtedly constantly enlarging, and consequently improved means will be hereafter obtained for acquiring a knowledge of the physiology of cells. At present,

* Max Schultze's *Archiv*, Band ii.

however, this must still rest on the physiology of muscle, as probably it will continue in great measure to do, even when it has received its greatest development. With regard to the specific functions of cells, we must limit ourselves to the general statement that there are cells possessing very various physiological functions, as nerve cells, muscle cells, gland cells, etc.; and, inasmuch as we are unable to conceive any functional process to take place in a cell without the occurrence of chemical processes, we must suppose that the specific functions of the cells in these several cases are essentially dependent on the nature of the chemical processes occurring in them. In the case of the muscles and in that of nerve cells, chemical investigations furnish us with no information beyond that of the dead tissue; whilst, in respect to gland cells, we do obtain some little insight into the nature of the chemical processes through an investigation of the secretion. Thus we know that there are cells which produce fat (mammary and sebaceous glands), others which develop pepsine, and further, that as a consequence of the activity of muscle and nerve tissue, acids are formed.*

From the results of the chemical investigation of protoplasm it would appear that, in all probability, it contains a considerable proportion of myosine (Kühne).† In some protoplasmic masses, protagon (Hoppe-Seyler, Fischer), in others glycogen, has been shown to be present, and in some few vegetable cells cholesterine‡ has been found.

It may be questioned, and remains to be shown, whether the substances which are obtained from cells after their death are pre-existent in them during life, or are only the products of disintegration. Hermann is of opinion that myosin is one of these products of disintegration. Of the nature of the functions fulfilled by the water and other inorganic compounds that exist in protoplasm, we know absolutely nothing.

Structure of Cells.—Brücke§ described a system of lacunæ in the salivary corpuscles, the cavities of which he thought were occupied by an intracellular fluid. He stated that the same appearances were presented by the protoplasm of the vegetable cells composing the stinging hairs of the nettle. Heidenhain‖ held the same opinion, and further maintained that the intracellular fluid was moved by the protoplasm in the same way that the contents of the intestines were propelled onwards by the peristaltic movements of the intestinal walls.

The protoplasm of vegetable cells may be so arranged that it traverses the space within the cellulose wall like a spider's web, and in such case the spaces between the protoplasmic fibres are occupied with a fluid; or the protoplasm may be reduced to a thin layer lining the inner surface of the cellulose wall, the interior of which again is bathed with fluid. But this cell fluid is not to be confounded with that which occupies the inner spaces or lacunæ of the protoplasm itself.

It may be observed in the flask-shaped glands of the nictitating membrane of the eye of the frog, that the size of the gland cells undergoes considerable variation. Sometimes the cells project so far into the lumen of the tube that this is reduced to an extremely small diameter; whilst, on the other hand, the cells are sometimes so contracted that the gland appears like a bladder lined with a simple layer of epithelium. These differences

* Du Bois, Funke.
† See Kühne, *Lehrbuch der Physiologischen Chemie.*
‡ Hoppe-Seyler, *Med.-Chem. Untersuchungen.*
§ *Ueber die sogenannte Molecular-Bewegung.*
‖ *Studien des Physiologischen Instituts zu Breslau*, Heft ii.

are not easy to comprehend, except on the supposition that the gland cells have by contracting expressed fluid from their interior.

It is also probable that at different times the protoplasm contains a greater or smaller quantity of fluid, and that under particular circumstances —by contraction or shrinking—it may thus be reduced to extremely small dimensions.

Another question which remains to be solved is whether we have grounds for admitting that, independently of the intracellular fluid, there exist any differences in the structure of the protoplasm.

Optical examination has not as yet enabled us to draw any conclusion on this point. Hitherto protoplasm has only been observed to be a body refracting light singly; or, more correctly speaking, no part of it has been observed to possess doubly refractive powers. When such a peculiarity has been observed, the protoplasm has been considered to be modified in order to fulfil some special purpose.

I am myself inclined to believe that two functionally different substances are present, and am supported in my opinion by the circumstance that I have learned to recognize two active conditions: one in which the cell is dilated, as after immersion in water; and one in which it is contracted (shortened).

But even if the dilated condition, as on Hermann's hypothesis, is to be regarded as the condition of rest, we must from this point of view also admit the existence of two functionally different substances.

In the present state of science we must acknowledge that we are unable to see any differentiation of parts under the microscope, nor does experiment furnish us with any ground for admitting the existence of a definite arrangement of parts differing in their physiological properties. At the same time, those cells, or cell derivatives, must of course be excepted in which we are able to recognize any definite peculiarities appearing to be associated with the performance of a specific function. The optical peculiarities of transversely striated muscular fibres, and the apparent structure perceptible in ganglion cells, must doubtless be regarded as dependent on differentiation of structure. Such instances as these are referable to the class of protoplasmic masses modified for the performance of some special function.

In reference to the boundaries of a cell, the state of our present knowledge has already been given in the introductory portion of this section. We hold that the external limiting layers of protoplasm may undergo both chemical and physical changes, and there will then be produced a membrane that, compared with protoplasm, is of firm consistence. The recognition of a double contour line in the uninjured cell is indispensably necessary to prove the existence of an investing membrane. Brücke remarks in reference to this point, "The difference between the density of the surrounding medium and the cell, even when no investing membrane is present, will cause the appearance of a boundary line. But it is only from the presence of a second contour that we are able to recognize a difference in density between the investing substance and the contained material. It is self-evident that the power of the instrument must not be pushed beyond its natural limits by the employment of strong oculars, as in that case a second contour line makes its appearance, not due to the structure of the cell, but consequent on defects in the optical apparatus we are using." If, moreover, a double contour line is observed after the action of reagents, no proof is afforded that a membrane existed during life. Kühne argued respecting the value of the double contour line as an evidence of structure, in the follow-

ing terms: "If an amœba were to surround itself by a broad hyaline border, not regularly defined internally, I should not be surprised if a reagent like acetic acid, which made this border suddenly shrink whilst under observation, were to cause the appearance of two wrinkled, closely approximated contour lines; and if I knew that this border was previously mutable, I should not believe the solid membrane, originating in the action of acetic acid, was previously present as an investment of the outer hyaline layer."

Many cells of the integuments possess distinctly perceptible membranes, as in the case of the mucous cells on the surface of fresh-water fish, first described by Leydig, and in a series of other analogous structures which F. E. Schulze * has collectively designated cup or chalice cells. F. E. Schulze distinguishes two kinds of cells, in one of which the membrane (theca) is completely closed, whilst the other exhibits a roundish, sharply defined opening.

At a much earlier date the epithelial cells of the villi had already been described by Brücke † as destitute of a membrane at their free extremity. It is still a subject of dispute whether this is a characteristic of all the epithelial cells, or occurs only in certain cup-like organs scattered amongst the ordinary cells of the epithelium.

The cell membrane may appear perfectly homogeneous, or it may possess pores (Leuckart).‡

The investing membrane may further present, according to F. E. Schulze, a want of homogeneity in consequence of becoming thickened by a secondary deposit. The basal part of the membrane of the epithelial cells of the villi, which is turned towards the lumen of the intestinal tube, must be regarded as a structure of this kind.

It is also here a disputed question whether this basal border is perforated by pores (Funke, Kölliker), or is composed of rods, giving it a striated appearance (Brettauer, Steinach).

THE NUCLEUS OF THE CELL.—Since R. Brown discovered the existence of a nucleus in vegetable cells, no remarkable advance has been made in our knowledge of this structure. Both Schleiden and Schwann held that the development of cells proceeded from the cell nucleus, and before as well as after their time the nucleus has always been regarded as a structure playing an important part in the propagation of cells. The objections have been already stated that were urged by Brücke against the view that the nucleus must be admitted as an indispensable attribute in our idea of a typical cell. We, in fact, know nothing with certainty respecting its physiological significance, nor regarding its physical peculiarities. It is, indeed, well known that, as a general rule, when a nucleated cell divides, the division first proceeds from the nucleus, which elongates, becomes hour-glass shaped, and ultimately constricted into two segments. Brücke adduces this as an answer to the statement, if any one were disposed to make it, that in all modes of propagation of cells the nucleus remains entirely passive. But in opposition to this line of argument is the fact that we are at present acquainted with non-nucleated cells capable of undergoing division, which is in itself a direct and sufficient answer to every statement that can be advanced in favor of the importance of the nucleus. It might indeed be said that when the nucleus is present it fulfils some important end in the act of propagation;

* Max Schultze's *Archiv*, Band iii.
† *Denkschriften d. Wien. Akadem.*, Band vi.
‡ See also F. E. Schulze, *loc. cit.*

but, in reply, it may be remarked that the division of nucleated cells has been observed where the nucleus has remained attached to the side. Remak * has made similar statements in regard to the red blood corpuscles, and very recently Weiss † also in reference to the protoplasm in the hairs of plants. Moreover, we know very little respecting the physical peculiarities of the nucleus. Reinhard has deduced its vesicular nature from its behavior in water, but we now know how little value must be placed on deductions of this kind. The presence of an investing membrane in many nuclei can be contested on the same grounds that render the presence of an investing membrane in various kinds of cells doubtful; many nuclei appear to be completely homogeneous, and are distinguishable from the surrounding protoplasm only by a single well-defined contour. Nuclei are, moreover, capable of undergoing manifold changes in form, and these may either be of an active or of a passive nature. At the same time we know that processes of budding and other similar changes cannot easily be conceived to occur in a vesicle enclosed by a membrane: when an amœboid cell is pressed flat, the nucleus also is compressed; and if the cell be again allowed to resume its original form, the nucleus similarly changes its shape. These are peculiarities that are certainly not very consonant with a vesicular character; still it is true that in many nuclei a double contour can be distinctly shown, as, for example, in many ganglion cells. It cannot be doubted, also, that such nuclei are invested by a limiting membrane of different nature from the contents; but we have no right to draw the conclusion from this, that the nuclei are usually vesicles. Rollett ‡ some time ago paid particular attention to the nuclei of the corpuscles, and described a peculiar formation of vacuolæ in their interior. More recently it has been stated, on the authority of observations made in this laboratory, that after induction currents have been applied to the corpuscles the nuclei will coalesce, which is very unlikely on the supposition that they consist of vesicles.

Our knowledge respecting the chemical characters of nuclei is also very obscure. Kühne § states that it is probable they contain an albuminous substance, and it is known that they present considerable resistance to the action of acids and alkalies; but this furnishes us with no satisfactory information respecting their physiological significance or chemical composition. Brücke remarks that the consistence of the nucleus is peculiar. On the cell theory it is believed to constitute the primary solid constituent of the cell, though no absolute proof has been obtained on the point. It cannot be denied that the nucleus is originally of very soft consistence, and that it subsequently becomes denser; nor can it be admitted that it ever exhibits any considerable degree of resistance in young cells.

It has been stated that, in all probability, the nucleus of the fecundated egg disappears. It is equally probable that the nucleus of the first segmentation mass is a new formation. But, as we possess no precise investigations respecting the disappearance of the germinal vesicle, we are also unable to derive the first nucleus of the segmentation mass of the egg of the frog from the nucleus of the unfertilized egg. In the unfertilized egg we meet with a vesicular nucleus. Under a strong lens it may easily be torn with needles, and then the membrane becomes apparent. The small sacculus contains a little clear fluid and a few granules. The first nucleus

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* *Entwickelungsgeschichte.* Berlin, 1855.
† *Die Pflanzenhaare.* Berlin, 1867.
‡ *Versuche am Blute*, *Wiener Sitzungsberichte*, 1863.
§ *Lehrbuch der physiologischen Chemie.* Leipzig, 1867.

of the segmentation sphere is, however, a completely homogeneous and apparently soft spherical body.

When it is said that the nuclear vesicles undergo solution, and are then again reformed, we have really not advanced one step in the solution of the question, for even this rests on no satisfactory evidence whatever.

What we do know is, that in its earliest stage the fertilized egg has no visible nucleus, and that the nucleus of the first segmentation sphere originates in protoplasm; that when very young, which must necessarily be its state in the segmentation sphere, the nucleus consists of a little mass of substance, in which, amongst other products of disintegration, albumen is found; lastly, that when old, and for this the unfertilized egg may be taken as an example, it may become converted into a vesicle.

Lionel Beale* has offered a plausible, though negative, explanation of the significance of the nucleus. He applies the term *germinal matter* "both to it and to protoplasm," and places them in opposition to *formed material* which constitutes the investing membrane. This view contains, at any rate, an indication that the nucleus and protoplasm possess certain characters in common.

Our knowledge of the nature of nucleoli is still more imperfect than that which we possess respecting the nucleus. To these also a special significance has been ascribed in the act of propagation, Virchow having quite circumstantially described his observation on the division of the nucleolus; and this, indeed, is the whole extent of our knowledge. Leydig refuses to admit that they are of any importance; but we cannot go so far as this, if we reflect that the nucleoli in many cases develop into a vesicle, in which still smaller nucleoli may be distinguished.

CELL GENESIS.—Schleiden advanced the theory that plants originate exclusively in homologous constituents. He proved that the nucleated cell was the only original component of the embryo of the plant, and that the development of all tissues might be referred generally to such cells. The formation of these cells takes place in a plasma, the nuclei first appearing, and then the investing membrane. The formative material, however, is commonly found within previously existing cells. Schwann, speaking of the origin of cells, remarks, "We have, in the first instance, a structureless substance, which, according to its chemical qualities and the grade of its vitality, possesses a greater or less capacity of effecting the development of cells."

Schwann was of opinion that the extra-cellular formation of cells, that is, their development in free blastema, was the most frequent mode of their production in animals. But the experience of embryologists was soon found to be in opposition to his views. The segmentation of the egg of the frog, already observed in 1824 by Prevost and Dumas, led to the statement made in the beginning of 1840, that the segments into which the egg breaks up are cells. This view was in the first instance defended by Reichert,† who believed that he was able to perceive a cell membrane in the several segments. Bergman‡ raised very solid objections to the existence of a membrane in this instance; and he quite correctly maintained that the spheres of segmentation are cells which are at first destitute of a cell wall, though they become invested by one at a subsequent period.

Henle also held that a close relation existed between the process of segmentation in the egg and the division of cells, and Kölliker interpreted the

* *The Structure of Elementary Tissues*, 1861.
† *Entwickelungsgeschichte im Wirbelthiere*, 1840.
‡ Müller's *Archiv*, 1841.

segmentation of the germ of cephalopods in the same manner. But this view of cell genesis was again very generally departed from. The merit of having defended it effectually must be ascribed to Remak* in particular, who has chiefly contributed to the abandonment of Schwann's doctrine of cell formation. Remak maintained with great steadiness that in the early stages of the development of the embryo no other mode of cell development occurs than by division.

To Remak also the merit is due of having established the same law in respect to the pathological development of cells. There is at the same time no doubt that Virchow played an important part in the extension of our knowledge in this direction, and that his well-grounded statement, made in 1855, "Omnis cellula e cellula," really constitutes the basis of our present cell theory.†

Whilst these fundamental propositions respecting the mode of cell formation in compound bodies were advanced and maintained on the one side, Pasteur proved by brilliant experiments that the statements made respecting the spontaneous origin of various organisms in fluids were erroneous, and that when all access of living organisms into such fluids was prevented, no development could be proved in any case to occur. Every one must admit that the general tendency of these facts is to disprove that a free extra-cellular formation of cells ever takes place. At the same time we are not justified in maintaining that such a mode of formation never occurs; it may, however, be said that at the present time not one observation has been made, incontestably demonstrating the existence of a generatio æquivoca.

We distinguish three forms of cell multiplication, one by fission, one by gemmation, and, lastly, an endogenous mode. According to Brücke, the last differs from the two former in the circumstance that the cells originate like embryos in the interior of the parent cell, and gradually increase in size, whilst in the other cases the substance of the mother cell breaks up into fragments, which constitute the second generation.

In the multiplication of nucleated cells by division the nucleus, as a rule, first divides; becoming elongated, then finger-biscuit shaped, and finally constricted into two portions, which recede from one another. The fission of the nucleus is not in all instances followed by division of the cell, though it is usually associated with the process of cell multiplication. Instances are known where cells become greatly enlarged, whilst their nuclei increase in number, either regularly or irregularly, to twenty or more; and in which, nevertheless, division of the cell itself has not been observed to occur. Division of the nucleus external to the cell, as has been already stated, has not as yet been shown to take place.

The formation of fresh nuclei within cells must be admitted to proceed, not only from fission of old nuclei, but from the growth of entirely new ones.

Development of nuclei proceeds in a manner essentially similar to that of cells when they undergo complete division.

As an example of endogenous cell multiplication, that which takes place in the eggs of insects may, according to Weismann,‡ be adduced; but whether the formation of pus corpuscles in epithelia (Buhl)§ is to be

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* *Entwickelungsgeschichte.* Berlin, 1852—1855.

† Virchow's *Archiv*, 1855, Band viii. Heft 1.

‡ *Entwickelung der Dipteren*, 1864.

§ The author of this paper has, as yet, had no opportunity to examine critically the communications made by Volkmann and Steudener, respecting the migrations of amœboid cells into epithelial cells, and the illusory appearances which may have led

regarded as an example of this mode, or of division (Remak), is at present doubtful.

If the entire mass of protoplasm contained within a membrane or capsule divides into two or more segments, we can no longer regard this as an endogenous mode of cell division, but as cell genesis by fission. Cartilage cells and the first two segmentation spheroids may be adduced as examples.

When a naked mass of protoplasm divides, the act is obviously to be regarded as one of fission. As an example of this the fission of the eggs in the ovaries of young cats may be adduced (Pflüger).

In multiplication by gemmation a little elevation first projects from the cell—a bud—which is subsequently separated by constriction of its base. An example may be seen in the propagation of the yeast fungus, in the development of the egg in Nematoids (Meissner), as well as in the budding of the germ of many holoblastic eggs (Salmofario, Stricker). The detachment of a cell from the maternal structures is a phenomenon of movement (Max Schultze). In regard to cell formation by fission, it has been ascertained that the protoplasm becomes partially contracted in the fashion of an hour-glass; the depth of the constriction continuously increasing until at length the protoplasm is divided into two segments. The whole process may be observed under the microscope in the fecundated egg of the frog.

No direct observations have been made as to the manner in which in endogenous cell genesis the daughter cells are set free in the body of the mother cell.

In many cases we are acquainted with the stimuli through the agency of which movements are occasioned. In the fecundated egg the spermatozoa must be regarded as the agents from which the first excitation proceeds. There can be no doubt, also, that in the act of fission a high temperature plays an important part (see above). In many other cases, however, the stimulus inducing the fission of cells is unknown.

The detachment of cells by constriction may be compared to the act of birth. Before detachment occurs by this mode the cell must have acquired a sufficient size, as otherwise material limits would soon be placed to the process of continuous fission. The essential feature of cell multiplication, therefore, consists in the capacity of assimilating new material.

The general proposition, then, that cells may increase by constriction and detachment, cannot be called in question. The segmentation of the ovum is an example which admits of no double interpretation. It may nevertheless be disputed whether certain cells of the adult organism are capable of increasing by constriction taking place in both the longitudinal and the transverse direction.

Since the migratory power of the white corpuscles has been ascertained, some doubts may arise whether any other cells besides these are capable of undergoing multiplication. With the exception of cartilage, in which there can be no more doubt of the occurrence of cell fission than in the fertilized egg, the structures which result from the fission of cells in the tissues of the healthy adult organization are not such as to render a mistake impossible. In cartilage we see the descendants of a parent cell enclosed in cavities of the solid matrix. But in all other tissues, where such firm boundaries are not met with surrounding families of cells, we cannot maintain with any degree of certainty that a group of two or four cells lying in close proximity to each

to the statement that an endogenous formation of cells takes place in epithelial cells. He, however, fully maintains the correctness of the statements of Buhl in regard to the development of cells from pre-existent epithelial cells, and has consequently adduced it as an instance.

other have originated in a previously existing mother of equal physiological value; for it might happen in such a case that the cells have migrated thither from some other part. It is even conceivable that the colorless blood corpuscles are destined for the regeneration of all the tissues of the animal body. Nor can any solid objection to this view be raised from the standpoint gained by a knowledge of the history of development. The blood proceeds, indeed, from a different germinal lamina to the epithelia, for example; but primarily all cells proceed from the segmentation spheres, and these again from the fertilized ovum. Lastly, who can determine what influences must be in operation to cause a segmentation spheroid to become an epithelial cell, and whether similar influences may not also act on young cells in the post-embryonal period?

Epithelial cells with two nuclei are often seen, and it is generally taken for granted that the division of the nucleus precedes the fission of the cell; but who can say that every division of a nucleus is followed by fission of the cell? It is possible that the division of the nucleus in an epithelial cell may be only an instance of arrest of development occurring in a cell which is no longer capable of undergoing division.

At the time when this article was published, the doubt cast by Cohnheim upon the fact of the pus corpuscles arising from the cells of connective tissue and of epithelium, had an important influence upon the opinion of histologists in Germany. On this account the results of the investigations of Goodsir, Redfern, Virchow, and his pupils, were believed to be founded upon incorrect investigation.

My later investigations* have, however, shown that the process of division of pus cells can be directly observed under the microscope, and that the proliferation of the cells of connective tissue by division, and of those of the epithelium by endogenous generation, are facts which cannot be disputed.†

It has in the mean while been ascertained in the case of a very easily observed object—the blood-vessels—that they are partially able to regenerate themselves—that fine processes grow out from the capillaries, which are themselves capable of becoming capillaries.

It is different with connective tissue. It cannot be doubted but that here some of the cells that migrate into it proceed from the blood; and the question must necessarily remain open, whether the connective tissue in those places where it maintains its ordinary local relations, is not usually regenerated by this means. W. Joung has expressed himself strongly in favor of this as being the mode of formation in the œdematous scrotum.

Our knowledge of the mode in which nerves and muscles are regenerated in the healthy organism is too limited to permit us to enter into any discussion respecting them. The main point of the question is connected with the growth of the gland cells, the epithelia, and the rete malpighii. Is the opinion justified, that the important discovery of Henle of the spontaneous growth of the rete mucosum can be shaken?

The development of epithelia from the cells of the connective tissue has already been maintained by many, as by Burkhardt, by Virchow, and by Förster. Very recently Pagenstecher‡ has stated that they may proceed from exudation corpuscles, and Biesiadecki says specifically that they come from colorless blood corpuscles. Two facts ascertained by the application of novel modes of investigation may lead to a decision on this point. The first is the presence of migrating cells between the epithelial cells (Recklinghausen),

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* *Studien aus dem Institute für experimentelle Pathologie.* Wien, 1869.
† MS. note added by Prof. Stricker.
‡ *Wiener Sitzungsberichte*, 1868.

and the second the circumstance that after the injection of finely granular coloring matter into the blood, it is also met with within the epithelial cells. The last is not a fact of much importance, since particles of coloring matter can be floated to whatever part a current of nutritive matter may set. The presence of migratory cells is a more important circumstance, but is likewise not very weighty. No one has hitherto observed that the migrating cells become changed into epithelial cells; it is not really derogatory to us to say that we are still ignorant of the significance of the migrating cells, and that we do not know what becomes of them. Were any one to maintain that the migrating cells are conjugation organisms, no stronger objection could be raised against him than against another who should maintain that the migrating cells are epithelia.

Recklinghausen* has advanced a theory respecting the conjugation of cells, which, however, on account of its brevity, scarcely allows us to judge of its value. The fact that the most beautiful example of cell fission, segmentation of the ovum, does not occur without fertilization, hardly enables us satisfactorily to determine the question whether the conjugation of cells is not a more frequent process than is generally admitted.

Forms of Cells.—No general statement can be made respecting the form of the amœboid cells, since the mutability of their shape is their distinguishing characteristic. It is to be presumed also that they present very different forms in death, and hence no certain conclusions can be drawn from the appearances presented by dead amœboid cells. These remarks are, however, only applicable whilst the cells remain suspended in fluid. In places where numbers are accumulated together they become flattened. Thus the segmentation spherules, whilst still in their natural position, are polyhedral with flattened sides, which are mutually opposed to the similar surfaces of others. Similar appearances are presented in most instances where soft and yielding cells completely fill a given space; but one axis may be longer than another, as is the case in the inferior layers of laminated epithelia, where they generally form prisms, or are arranged in the manner of palisades. The cells which are superjacent to them, on the other hand, are polyhedral, without any one axis being longer than another. The uppermost layers of laminated epithelia are usually flattened.

The cells of the laminated epithelium of the upper part of the respiratory tract are for the most part elongated, and present two principal varieties in form, one of which is that of a longer or shorter flask-like body, giving off a process from one of its ends, whilst the other is that of a fusiform cell with a relatively short belly and elongated attenuated extremities. Where the cells line the interior of cavities as a single layer, they appear either in the form of plates of different shape (endothelial cells of His), or of cells in which the long axis is predominant (cylindrical epithelial cells); or we may meet with various intermediate forms between plates and cylinders.

The cylindrical cells are not cylinders in a stereometric sense, but are frequently conical, with the base turned towards the cavity, whilst at other times they form cones, from the apex of which a process is given off. Cells may again present the appearance of being as it is termed ramified, or provided with numerous processes (bone cells, corpuscles of the cornea); or lastly, they may become extraordinarily elongated as in muscle cells.

A form of cell which must be regarded as quite peculiar, is that which is provided with cilia. The form of the ciliated cell varies to a considerable

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* Max Schultze's *Archiv*, Band ii.

extent, but the cilia are always limited to one portion of the surface, and constantly project with their free extremities into the interior of the cavity of the organ they line.

The cilia themselves may be of various length, and may on the one hand considerably exceed the long diameter of the cell, as occurs in those lining the renal capsules of some amphibia (Remak,* Duncan); and on the other may be so short that they only measure a fraction of the long diameter of the cell; it is in such cases especially that when at rest they give the appearance of a moderately broad hem or border to the cell. Again, not only the length but the thickness of the cilia varies; thus we find that the cilia on the superficial cells of the egg of the frog, after it has undergone segmentation, can scarcely be perceived even when magnified 400 times with a good instrument; whilst the cilia on the gills of the Anodonta are easily recognized near their base with a very low power.

Union of Cells with each other.—By the treatment of tissues with diluted solutions of nitrate of silver, as suggested by Recklinghausen,† we have acquired a knowledge of the means by which certain varieties of structure can be recognized, and we have also learnt that even when cells are apparently in contact an intermediate material is present, by which they are cemented to one another. Recklinghausen has by the use of this method rendered certain markings apparent in the finest lymphatics; and Eberth, Aeby, and Auerbach‡ have by similar means exhibited peculiar patterns in the blood capillaries, whilst similar lines may generally be brought into view wherever cells lie in apposition.

A difference of opinion exists in regard to the significance of the lines brought out by silver in the blood capillaries. Those who oppose the ordinary view base their opinion upon the history of development, from which we learn that the blood capillaries commence as solid fibres, and then become hollow; but we also know, through the investigations of Reitz,§ that the villi of the placenta commence as solid fibres, which subsequently become hollow, and that after the occurrence of an abundant proliferation of nuclei the sheath of protoplasm of these now hollow processes undergoes differentiation into cylindrical cells. We thus see that a considerable mass of protoplasm can become differentiated into cells.

The formation of the blood capillaries must be described in a similar manner; they commence after the fashion of a gun-barrel with smooth bore, but subsequently appear like the shaft of a chimney; cell boundary lines, or, more correctly speaking, lines of connective substance, being developed in their wall.

The consideration of this process teaches us that the cement is to be regarded as proceeding from the metamorphosis of the cell substance, and is therefore properly included in the series of intercellular substances. Cells may either present flat surfaces in apposition to each other, or they may present small processes, dentations, or striæ, by means of which they cling to one another like the bristles of two brushes.‖ They may also become attached to one another partly by means of flat surfaces and partly through the intercalation of the processes.¶ Inasmuch as the cement is included in the

* *Froriep's Notizen*, 1845.
† *Wiener Sitzungsberichte*, 1867.
‡ *Centralblatt*, 12, 13, 14, 1866.
§ *Wiener Sitzungsberichte*, 1868.
‖ Max Schultze, *Centralblatt*, 1864, No. 12.
¶ F. E. Schulze, *loc. cit.*

series of intercellular substances, it must be admitted that there is no fundamental morphological difference between the material connecting epithelial cells, endothelial cells, and the cells of the connective tissues; in all these we have to do with metamorphosed cell substance, by means of which the morphological elements are united.

Besides the mode of union by means of intercellular substance, we are also acquainted with a mode in which cells unite through the intermediation of processes, and we have already noticed that, under certain circumstances, cells may become fused together, an occurrence that may take place whilst they are yet living. We cannot therefore doubt that the protoplasmic masses are capable of directly uniting with one another. Nevertheless the microscopic proof of the direct fusion of cells has not been quite satisfactorily demonstrated. It is possible that the union may be established by means of cement, but this, up to the present time, has not been clearly shown.

From a physiological point of view, however, we must admit that fusion of the processes of nerve cells may take place; at all events, it would be in opposition to our experience respecting the conduction of nervous force, were we to admit that any cementing substance intervened between the individual nerve cells.

With the exception of the nerve cells, the above-mentioned objection holds good for all supposed or actually proved instances of cell union.

Classification of Cells.—Cells are usually classified in accordance with their physiological function. This, however, is not a very satisfactory mode, since we are still ignorant of the functions of many groups of cells. For example, we have no precise knowledge of the functions fulfilled by the colorless blood corpuscles, and it is moreover improbable that all the cells distributed over the surface of a membrane, as epithelial and investing cells, should possess identical functions. We find, for instance, that between the epidermal cells of the fish there are peculiar clavate cells which have been described by Max Schultze, and circular-headed cells by F. E. Schulze; whilst wandering cells, chalice-like cells, etc., have been observed by others. All these forms of cells are probably functionally different, and cannot, according to our ideas of classification, be included under the single head of epidermal cells.

It has been thought that a primary ground of classification of cells might be drawn from some of their morphological characters or genetic peculiarities, but we shall see that none of these characters are sufficient to attain the end in view.

In reference to function we must distinguish nerve cells, muscle cells, red blood cells (respiratory organisms), gland or secreting cells, ciliated cells, and, lastly, connective tissue cells, as amongst those whose function essentially consists in the construction of the framework of the body. With these may also be enumerated those cells, the function of which we deduce from their situation and arrangement; to this group belong the cells of the epidermis, with the endothelia and those cellular investments of the mucous membranes to which we can ascribe no specific secretion, as the epithelium of the œsophagus and of the urinary tubuli. The function of these may be considered to consist in forming the boundaries of cavities, and in protecting important organs, as the cutis, against external injurious influences; but at the same time we must admit that in regard to their morphological differences we are but partially acquainted with their function. Lastly, the colorless lymph and blood corpuscles may be alluded to; of these we know

indeed that in all probability they are destined for the regeneration of the red blood corpuscles, but we know also that they fulfil other and quite different objects.

Cells can be classified according to their genesis, that is, according to the germinal membrane from which they originate; nevertheless, however successfully the classification of investing cells into epithelia and endothelia (His) may be effected on this principle, it is not capable of wider application. The cells of the cutaneous glands, for example, would have to be separated from those of the intestinal glands, because the former proceed from the upper, the latter from the lower, germinal membrane. Moreover, all cutaneous glands would have to be included in the series of epidermal cells, all epithelia in the series of secretory cells, and, lastly, connective tissue, muscle, and blood would require to be combined in one and the same category. If no objection can be raised to many of these systems of arrangement, it is at least impossible to regard any of them as perfect.

Morphological peculiarities alone constitute a ground for the formation of subdivisions, and these will be considered in subsequent chapters.

Formative Activity of Cells.—The recognition of the fact that the animal body, excluding the ingesta, consists only of cells, or of cell derivatives, constitutes one of the most valuable conclusions arrived at by Schwann.

The next chapter will place before the reader, in a more extended form, the facts on which he grounded this statement. We can here only refer to the general importance of cells in the animal body, and in regard to their formative activity it may suffice to point out that every organized portion of the animal body which is not a cell must originate in or from cells. In addition to the organized constituents of the animal body, chemical compounds are also present in it, which, so far as they have not been introduced in those forms, must be regarded as the products of cell activity; but we cannot ascribe the non-organized bodies, even though they may be deposited as solid compounds, to the formative activity of cells. To this account we only place those materials which become a portion of the organized constituents of the animal body through cell metamorphosis.

Changes of Cells in Death.—It is difficult in many cases to decide whether a cell still lives; it is not sufficient to know that the preparation has been taken from a living animal, or from the body of one which has only been dead for some hours. If the cells exhibit no amœboid movement, and if, on the other hand, they are not taken from putrefying portions of the body, the determination is difficult, and sometimes even impossible. In the present state of our knowledge, chemical reagents do not enable us to arrive at any positive decision, unless their action is sufficiently slight to excite movements, but not to effect complete destruction. This is indeed true of all other agents, for they can only furnish us with information in regard to the life of the cell when they produce changes which our experience teaches us are ascribable to life; on the other hand, it is often easy to determine that a particular cell is dead. The greater number of chemical reactions refer to the phenomena exhibited by dead cells. The forms which cells killed by chemical agents present are so various that they cannot be enumerated, but the most important have been treated of in the first chapter.

If the cells have been killed by powerful electric currents, by a high temperature, or by mechanical violence, the determination of their condition, after what has already been said upon the effects of these agents, can no

longer be doubtful. But if no remarkable alterations of form (flattening, tearing, bursting), no remarkable physical alterations (cloudiness, coagulation), and lastly, no definite change resulting from the action of the fluid in which they have been preserved, furnish indications of the death of the cells, no scientific value can be attributed to any statement made respecting it.

CHAPTER II.

THE CONNECTIVE TISSUES.

By A. ROLLETT,

PROFESSOR OF PHYSIOLOGY IN GRAZ.

It has become customary in histology to associate together a series of tissues under the term connective tissues. From these tissues all those portions of the animal body are formed, which can be regarded in the most general significance of the terms as the basement membrane, supporting layer or investment for epithelial structures, blood, lymph, muscles, and nerves. In the Vertebrata the group of connective substances includes connective tissue, cartilage, bone, the tissue of the cornea and dentine.

The connective tissues are developed from the middle germinal layer, in which blood and muscle also originate. The typical connective substances are recognized histologically by the circumstance that they contain extensive and continuous layers of material (intercellular substance), which, when compared with the cellular structures distributed through its substance (protoplasma), or the morphological elements in other tissues, always appears as a more passive substance, and one which participates but slightly in the processes characteristic of life. These masses consist for the most part of gelatine-forming substances, such as collagen, chondrogen, and ossein. The connective tissues frequently pass by substitution or genetic succession into one another; they appear therefore to be morphologically equivalent; so that in many instances certain organs, or parts of organs, belonging to animals nearly allied to one another, are formed sometimes of one, sometimes of another of these tissues.

Even if our knowledge of such facts disposed us to collect the tissues into a single category, this is still not the immediate and primary reason that has led to the formation of a group of connective substances. This last has become customary since the experimental investigation of these tissues has shown that they present similar modes of development, and possess consequently an homologous significance in regard to their microscopic constituents.

The fate of the connective tissue theories thus originating has been very variable. Reichert * first appeared with his doctrine of continuity of substance. According to this the connective tissues contain a matrix, originating in the fusion of cells, or of certain portions of cells, with an amorphous intercellular substance. Reichert associated with this mode of development the peculiar connective tissue formerly regarded as fibrous, but considered by him to be destitute of structure, and pointed out that in both there was an absence of any apparent boundary line between the allied tissues where they were in contact with one another, or, as he expressed it, there was a "continuity" of their matrix.

This theory was, even from the first, strongly opposed by Henle,† and did not in the first instance meet with general acceptance. If the views on the

* *Beiträge zur vergleichenden Naturforschung*, etc., Dorpat, 1845.
† Canstatt's *Jahresbericht*, 1845, Bd. i., p. 55; 1847, Bd. i., p. 44.

absence of structure in connective tissue taught by Reichert, and now disproved, found certain adherents, amongst whom Virchow himself may be included, it can scarcely be held, as however is frequently done, that the connective tissue theory promulgated by Virchow in 1850, was only a modification of that of Reichert. We are indebted to Virchow* and Donders † for directing attention to the persistence of cells in mature connective tissue. Virchow, whilst he regarded the cells of connective tissue (connective tissue corpuscles) as the analogues of the cells of cartilage and bone, constructed a simple scheme‡ for the structure of connective tissues; and, upon the other hand, sought to attribute to the excitation, growth, and proliferation of these tissue cells a series of the most important pathological processes, and was thus led to the profound views contained in his cellular pathology.

According to Virchow's idea the greater part of the tissues belonging to the group of connective tissues consists of intercellular substances, the latter indeed varying in regard to their chemical nature in the several members of the series, and containing variously formed but similar cells imbedded in their substance. The views of Virchow obtained general acceptation. The special methods which he employed in his researches caused him, however, to describe forms which had nothing to do with connective tissue cells, and induced him in the case of connective tissue, as had been done by earlier inquirers in regard to osseous tissue, to admit the existence of cell processes frequently anastomosing with one another, which he regarded as forming a plasmatic canal system traversing the tissue in all directions. Henle § in both instances expressed determined and persistent opposition to the existence of connective tissue corpuscles in the sense understood by Virchow. The point in question required an exact appreciation of appearances exhibited under the microscope, and the final result was that inquirers for the most part convinced themselves of the existence of persistent cells in mature connective tissue.

In the mean while, however, through the investigations of Max Schultze,‖ Brucke,¶ and others, the doctrine of cells founded by Schwann, and up to that time generally received, experienced some important modifications. It was no longer possible to describe animal cells as uniform elementary parts of a vegetative character, constructed according to a certain scheme. The new opinions held in regard to the structure of connective tissue substances could not remain without influence upon the general conception of a cell. Still more directly was the connective tissue question affected by the views which were coincidently expressed by Max Schultze upon the solid intercellular substances of the animal tissues. Up to that time the majority of observers regarded the matrix of hyaline cartilage as the prototype of an amorphous intercellular substance, and indeed very generally as the starting-point for its consideration. Max Schultze, on the other hand, opposed to this the hitherto little regarded views of Remak and Fürstenburg, on the matrix of cartilage, and sought to show that we have not here to deal with an intercellular substance in the sense of a hardened secretion between the cells, but rather that the so-called intercellular substance, from its very

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* *Würzburger Verhandlung*, Bd. ii., pp. 154 and 314.

† *Zeitschrift für wissenschaftliche Zoologie*, Band iii., p. 348.

‡ *Cellular-Pathologie.*

§ Canstatt's *Jahresbericht*, 1851, Bd. i., p. 22; 1852, Bd. i., p. 20; 1853, Bd. i., p. 8. See also Henle, *Jahresbericht* for 1858, p. 53; 1859, p. 28.

‖ Reichert and Du Bois Reymond's *Archiv*, 1861, p. 1.

¶ *Sitzungsberichte der Wiener Akademie*, Band xliv., 1861, p. 381.

commencement, proceeds from the protoplasm of the cells. This, in its turn, immediately led to renewed investigation respecting the genetic significance of the matrix of bone, and of the fibrillar substance of connective tissue.

Max Schultze * forthwith stated his opinion that the fibrillar substance of connective tissue originates from "embryonal cells composed of protoplasm, and destitute of any investing membrane, which have amalgamated with one another." A thin layer only of the protoplasm remains lying around the nucleus of the primary cell, representing with this nucleus a connective tissue cell, destitute of cell wall (connective tissue corpuscles). It should also be mentioned that, quite independently of the discussion maintained on these points in Germany, similar views respecting the development of connective tissue were expressed in England by Beale.† According to Beale's peculiar terminology, connective tissue is originally composed of elementary parts (cells), which consist of germinal matter (Keimstoffe, protoplasm); but subsequently a part of the germinal matter is converted into formed material (in connective tissue the fibrillar substance), which was itself in the first instance germinal matter, and was developed at the cost of that matter. Beale, whose statements were of a somewhat general nature, admitted a similar genetic relation between the matrix of bone and cartilage, and the cells of those tissues.

Waldeyer ‡ especially endeavored to confirm these views, in the case of bone, by his beautiful researches on the process of ossification. It is obvious that, in the event of the above-described mode of development being demonstrated in the several cases of bone, cartilage, and connective tissue, a similar genetic agreement for all these tissues, though undoubtedly in a different sense from that advanced by Virchow, would also be obtained. But to what extent satisfactory replies have been given to these questions will hereafter receive consideration when these tissues are severally described.

As observers gradually acquired these views respecting the histogenesis of the connective tissue substances, a new starting-point for important general considerations respecting the living processes taking place in connective tissue was obtained, in quite another mode, by the investigation of living connective tissue. Von Recklinghausen § demonstrated that, in living connective tissue, cells are present which agree in their characters with the white blood corpuscles (lymph or pus corpuscles), and, in consequence of the amœboid movements they are capable of performing, constantly change their situation in the tissue. Von Recklinghausen further proved that when suppuration occurred in connective tissue, in opposition to the doctrine propounded by Virchow of the formation of pus by multiplication of the tissue cells, a migration of these movable cells from without into the substance of the tissue must be admitted to take place. These facts have attracted a proportionately greater interest since Stricker‖ established the permeability of the walls of the vessels for red blood corpuscles. Cohnheim,¶ indeed, has recently referred to the older observations of

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* *Loc. cit.*, p. 13.

† *The Structure of the Simple Tissues of the Human Body*, translated into German by V. Carus. Leipzig, 1862, pp. 36, 96, etc.

‡ *Archiv für Mikroskopische Anatomie*, Bd. i., p. 354.

§ Virchow's *Archiv*, Bd. xxviii., p. 157.

‖ *Sitzungsberichte der Wiener Akademie*, Bd. lii., p. 379.

¶ Virchow's *Archiv*, Bd. xl., p. 1. Kosinksi, *Wiener Med. Wochenschrift*, Nos. 56 and 57, 1868.

Waller * on the relation of the white blood corpuscles in inflammation, which have hitherto remained unnoticed; and, supported by these older and his own more recent observations, has propounded the view that purulent infiltration really consists only in the migration of colorless blood cells through the vascular walls into the tissues. The relations thus shown to exist between the blood and the tissues must, as we shall see, still be held in view in discussing other questions bearing upon the connective tissue substances in the following pages. For this reason, the three typical connecting substances—connective tissue, cartilage, and bone—will now be separately described. The consideration of the peculiar tissue of the cornea, on the other hand, with dentine, and some others, will, on account of their more limited and special distribution in certain organs, be postponed to a later period.

Of Connective Tissue.

A series of various forms of tissue must be included under the term connective tissue. This name was originally given in 1830, by Johann Müller,† to the tela cellulosa of the older anatomists; but as at that time observers‡ had already convinced themselves that this tissue is essentially composed of very fine fibres, which may be proved to be the chief constituent of tendons, ligaments, membranes, and other formed portions of the organism, all these tissues, together with the tela cellulosa, were included amongst those portions of the organism which are composed of connective tissue. Formerly, however, the description of this tissue was limited to a fibrous form of the tissue, possessing very definite histological and chemical characters.

This limitation has, however, been greatly extended by custom, and just as, in consequence of their functional agreement and continuity of substance, a series of microscopically different structures are combined under a common term—as muscle, nerve, etc.—we are on similar grounds led to a general application of the term connective tissue, and to distinguish its several forms. Amongst the microscopic morphological constituents thus distinguishable in connective tissue may be enumerated cells; networks and trabeculæ, developed from cells consisting of peculiar delicate unbranched fibres (connective tissue fibrils), for the most united into fasciculi; and, lastly, fibres which are differentiated from those above named by the resistance they offer to the action of acetic acid and alkalies, by their repeated division, by their forming networks, and by their fusing into lamellæ (elastic fibres).

Of the Cells of Connective Tissue in General.

In all connective tissues, whether obtained from an adult organism or from one in process of development, cells may be found, the number of which in different instances varies within very wide limits. In the cells obtained from connective tissue we observe so many different conditions of activity, development, metamorphosis, and disintegration, and know so little respecting their material composition and changes, their physiological peculiarities, and their genetic connection, that it is impossible to give a general description, which shall be applicable to all the forms they present. On the other hand, a few facts may be here stated which are of general importance in

* *Philosoph. Mag.*, Vol. xxix.
† *Handbuch der Physiologie*, Bd. i., p. 410. Coblentz, 1835.
‡ Jordan. For the doctrines of G. F. Treviranus (1816), H. Milne Edwards (1823), see E. H. Weber's edition of Hildebrandt's *Handbuch der Anatomie.* Braunschweig, 1830.

regard to the cells contained in connective tissue, and will thus enable us to take a broad view of the subject; and, in the first instance, the researches commenced by Von Recklinghausen* and Kühne † on the living tissue may be adduced.

In the living body the cells of connective tissue may be observed wherever it is possible to make thin sections adapted for high magnifying powers quickly, and without the employment of any hardening process. They may then be subjected to microscopic investigation, after the addition of some indifferent fluid, as serum, the aqueous humor, and serum containing iodine, especially with the aid of a moist chamber. In specimens so prepared, Von Recklinghausen first observed the presence of migrating cells in the connective tissue; and after he had demonstrated that the cells of pus possess amœboid characters similar to those which were already known to exist in the white blood—and lymph—corpuscles, he pointed out that pus corpuscles lying in this tissue—as, for example, in the inflamed cornea or in the mesentery of the rabbit—possessed the same mobility. He further found that young cells, agreeing in their characters with the white blood corpuscles, are present in small numbers in the healthy cornea of the eye, in the tail of the tadpole, in the peritoneum, and in various other places.

Where such cells are found in connective tissue, they are characterized by their relatively rapid change of form, and by their coincident and considerable changes of place in the tissue, on which account they were designated migrating or wandering cells ‡ by Von Recklinghausen. In regard to these cells, we must refer to the general doctrines of cells already given, and to the section on the blood. It may, however, here be remarked that they may be easily differentiated from other movable cells occurring in the animal body. Amongst the various cells present in the connective tissue of the fully developed and adult organism, these white blood-corpuscle-like cells are best characterized by the circumstance that they alone deserve to be named amœboid cells. These cells, if the expression may be allowed so, are the most active, and present the most variable forms that are ever observable in this form of tissue. From the researches which Stricker § made on the permeability of the walls for the morphological elements of the blood, and those of Cohnheim ‖ and Hering ¶ on the exit of the white blood corpuscles through the vascular wall into the tissue, the derivation of the migrating cells of the connective tissue from the blood has been certainly demonstrated in some particular instances, and rendered highly probable for all.

The migrating cells may be most conveniently observed,** and differentiated from the other cells contained in the tissue, in the tail of the living tadpole. In this object Golubew has frequently exhibited to me the migration of these structures from the vessels.

In the case of the blood of the frog, it may be shown that the amœboid cells it contains are subservient to the regeneration of the red corpuscles, into which they become transformed by a process all the stages of which may be completely followed.†† We must therefore ask whether any further

* *Loc. cit.*
† *Untersuchungen über das Protoplasma und die Contractilität*, p. 109. Leipzig, 1864.
‡ *Wandernde Zellen.*
§ *Sitzungsberichte der Wiener Akademie*, Bd. lii., p. 379.
‖ *Loc. cit.*
¶ *Sitzungsberichte*, Bd. lvi., p. 691.
** Von Recklinghausen, *loc. cit.* F. E. Schulze, *Archiv für Mikroskopische Anatomie*, Bd. ii., p. 378.
†† Golubew, *Sitzungsberichte der Wiener Akademie.* Sitzung vom 16th April, 1868.

metamorphosis occurs in the amœboid cells of the connective tissue; and on the answer we obtain depends the still more important question, whether all or much of the development and growth of connective tissue is to be referred to a proliferation of the cells forming the original mass of the tissue, or whether, as has already been shown to occur in neoplastic pathological formations, those amœboid cells participate which originate in localized germ masses in the organism, and have then migrated into the tissue.

We now turn to those cells of the connective tissue which are capable of being distinguished from the amœboid cells, and meet, in the first place, a peculiar material obtained from the living tissues, which has been made known by the researches of Kühne.* I allude to that kind of connective tissue which apppears in the form of perfectly transparent membranes between the muscles of the leg and thigh in the frog. According to Kühne, several varieties of cells can be here distinguished, differing from the migrating cells. They all appear to be formed of granular material, but some are characterized by being surrounded with a very finely granular cloud, by which they are distinguished from the transparent matrix; that is, traversed only by a few fibres. Others, again, appear to be formed of a material containing larger strongly refractile granules. The coarsely granular cells possess, for the most part, an elongated form; the nucleus, which occupies the broadest part of the cell, is elliptical, transparent, and bounded by a double contour line, or it may appear in the thickened portion of the cell, indistinctly defined, and equably covered with the granular mass. It may be noticed that such coarsely granular cells are often connected by their apices in twos and threes together. Besides the fusiform coarsely granular cells, there may frequently be seen similar cells of more compressed and rounded form.

The finely granular cells are either provided with a distinct oval and clear nucleus, or their contents may appear to be accumulated at one point around a body resembling a nucleus. The finely granular cells give off a variable number of processes differing in their length and thickness; and these, radiating in various directions, frequently join. When these finely granular cells are long and carefully observed, slow changes of form may be seen to occur; such changes are, however, much slower than those undergone by the migratory cells, and do not lead to any remarkable change of place. In the same preparation, migratory cells are also frequently seen, and the difference in the mode in which the movements are performed, as well as other peculiarities of both forms of cells, may be easily ascertained by direct comparison. The migratory cells are generally smaller, and the addition of acetic acid brings one or several small round nuclei into view, whilst all other cells, after the action of acetic acid, present distinct nuclei of larger size and more oval form.

Kühne has endeavored ineffectually to excite movements by means of electricity in the different kinds of cells he has described. If we apply a large induction apparatus (brought into activity by means of chromic acid and carbon, with a primary coil of 160 turns, a nucleus of iron wire, and a secondary coil of 6,245 turns, thrust quite home), and examine the effects of a few shocks, allowing a few minutes to intervene between each, it will be seen that the cells with finely granular protoplasm, withdrawing their finer processes, contract gradually into round strongly granulated masses; or they may only retract their longer processes to a certain extent, without

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* *Untersuchungen über das Protoplasma und die Contractilität*, p. 109. Leipzig, 1864.

causing them entirely to disappear, so that they become knotty, whilst the body of the cell containing the nucleus assumes a rounded form. A return from this altered condition to the original form has not been observed. The above-mentioned appearances constitute a further difference, distinguishing these from the migratory cells; the latter show, as in the case of the white blood corpuscles, when such shocks have been transmitted through them, an alteration in their mode of movement, or a sudden retraction of all the processes, and the assumption of a round form; after which they soon again recommence their former movements (Golubew).* In similar preparations from newts and salamanders, the appearances presented are the same as in the frog. In warm-blooded animals, a loose connective tissue can be obtained from the surface of the muscles in the form of thin laminæ; this contains, indeed, a larger number of fibres than in the frog, but is nevertheless well adapted for the observation of the cells that accompany it. The masseter of a recently killed rabbit or guinea-pig may be exposed, and after division of the fascia a portion of the connective tissue immediately investing the muscular fibres may be removed with scissors, and in this coarsely granular and cylindrical protoplasmic masses may be seen, containing a more or less distinct elliptical nucleus. Most of these cells contain a few granules of considerable size, which in one focus appear as dark pigment molecules, and in another seem to possess a bright centre.

Besides these coarsely granular cells, other very finely granular ones appear, which are for the most part more delicate and pale, and frequently exhibit fine radiating strongly refractile striæ of greenish tint. These easily overlooked, delicate, and proportionately large structures may best be recognized by their very distinct large vesicular nuclei.

Cells similar to those above described may also be found in the looser connective tissue of other muscles, in the subcutaneous tissue, and elsewhere.

If we pass from the examination of such delicate and loose connective tissue to the thicker and denser masses of the same tissue, various objects may be found which are adapted for its examination in a physiologically fresh condition. For this purpose the thin fasciæ of the frog and of warm-blooded animals are very appropriate, as are also the thin flexor tendons of the fingers and toes of the frog, newt, or salamander, which can be drawn out at one end from the double-capped fingers or toes. We may here see small fusiform granular masses containing delicate elongated nuclei intercalated amongst the parallel fibres of the several fasciculi. In comparison with the cells of the looser connective tissue, the granular substance of these cells appears to be much reduced in amount. In the above-mentioned tendons there also appear more rounded, serially arranged, and somewhat flattened cells with well-defined round nuclei. These do not lie upon the surface, but in the elongated fusiform interstices of the fibrous material. Such chains of cells have their greatest dimensions in the broadest part of the fusiform spaces. At the border of the above-mentioned tendons a thinner portion of the investing connective tissue is generally to be found traversed by numerous fibres in which the above-described cells of the loose connective tissue can be very well observed; but besides these, stellate cells may also be seen, which give off sharply bordered trabeculæ, that present a smoother appearance, give off branches, and may be followed for a considerable distance between the fibres of the investing connective tissue. The behavior of the cells present in connective tissue, when treated with chemical reagents, now requires a more extended examination.

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* *Loc. cit.* See the chapter *On the General Doctrines of Cells.*

The migratory cells are best adapted for investigation in this respect, on account of their having been already so long known as the white corpuscles. In regard to other cells, the observations made by Kühne on his specimens may be adduced. Water acts energetically on the finely granular cells in particular, the granular material contracting around the nucleus, and only remaining connected with the surrounding parts by means of a few anastomosing processes. The meshes of the network thus formed are clear, and a few granules presenting molecular movements may be observed in their interior. The nucleus first swells up, and exhibits vacuolæ in its interior, and, after undergoing many changes of form, finally contracts into a shrivelled corpuscle.

The network brought into view by the action of acetic acid is darker, and the nucleus subsequently appears to be filled with dark granules.

In diluted solutions of potash and soda the nuclei of all the cells in such specimens are distinctly defined. They appear pale and vesicular. The cells acquire a border, seam, or doubled margin; the granular portion of the cell diminishes in size with the formation of larger or smaller clear drops, and, in consequence of the coalescence of these drops, vacuolæ become developed, the formation of which was also observed by Kühne after the action of diluted acetic acid.

As has been above stated, but few objects are well adapted for the examination of connective tissue in the fresh state. In the case of all thick, soft, and easily alterable masses, or in those that are more dense and opaque, in order that the cells may be exhibited, preparations must first be made by section, or by teasing up the tissue with needles, and subsequently agents employed by which they may be hardened and rendered transparent. The objects that are capable of being examined in a physiologically fresh condition may then be used as test objects, and a comparison instituted between them.

The best solutions are those of chromic acid, and especially that recommended by Müller,* consisting of two and a half parts of chromate of potash, one part of sulphate of soda, and 100 parts of distilled water. If the latter be applied to the test object, which has just been obtained in the perfectly fresh condition, treated only with an indifferent fluid, and placed in a moist cell, it may remain as long as may be desired in contact with the reagent, and the changes produced by the hardening solution may be examined from time to time. We may then convince ourselves that Müller's solution preserves the cells in a nearly unaltered condition, so far as regards their external appearance. They indeed become slightly shrivelled, and the contour lines become smoother and more sharply defined; but the larger processes of the cells are completely preserved. The granular character of the cell substance becomes somewhat more distinct; but there is no more evidence of the presence of a membrane investing the cells as indicated by a double contour line now than in the fresh state. In all the cells the nucleus either becomes distinct, and presents a vesicular appearance with a coagulated mass in its centre, or loses its double contour, and appears coarsely granular throughout its whole substance. The imbibition of a solution of carmine renders these appearances still more distinct. From such hardened connective tissue, isolated cells may be obtained by teasing out the tissue with needles, and they may then present very various forms. The most common is the fusiform, very beautiful specimens of which may be obtained from the tendons of children and young animals, where they are both more

* See also Langhans, *Würzburger Naturwissenschaftliche Zeitschrift*, Bd. v., p. 86.

numerous and more easily isolable than in those of adults,* and also from the connective tissue sheaths of the nerves in man and mammals. They may be obtained with equal facility from the neurilemma of the nerve trunks of frogs, still better from salamanders and tritons, and best of all from the proteus, where they are extraordinarily large, and can be isolated with the greatest ease; such isolated fusiform cells often possess very long nuclei, which are covered only by a thin layer of cell substance. Fusiform cells of remarkable size may be obtained from the tendon of the sterno-radial muscle (pre-sterno-claviradial of Dugés). They are here of a greater length than in any other tendon of the frog, and with their elongated nuclei call to mind smooth muscular fibre. The nucleus of these cells is on the average 0·0192 millimetres long and 0·0032 millimetres broad. Their length is difficult to determine, on account of both extremities ending in very fine and long processes. I found the length of cells, which had been completely isolated from the surrounding fibrous mass, to be in some instances as much as 0·0960 millimetres. In the tendons of man, isolated fusiform cells were 0·0320 millimetres long; the length of the nucleus amounted to 0·0160 millimetres, and its breadth to 0·0048 millimetres.

The cell substance of the fusiform cells is broader in young animals and in embryos, and here the cells frequently give off branched processes, which communicate with those proceeding from other stellate cells. The fusiform cells are less abundant in the fasciculi of the connective tissue of adults than was formerly supposed. They are remarkably developed in the cornea. In embryonic connective tissue they are very numerous, and repeatedly communicate by means of their processes.

We also meet with anastomosing stellate cells in the adult in the more independent connective tissue formations, occupying the interspaces of the fibrous connective tissue, or in places where fibrous connective tissue is altogether absent. From a general review of the cellular structures found in connective tissue, it is apparent that, beginning with the young cell, we have to deal with a series of cells in various stages of development.

The importance of any statement made in regard to the size and form of the cells, on which so much stress was formerly laid, will be less in proportion to the degree of mobility possessed by the cells when in the perfectly fresh condition.

It would, however, be decidedly going too far, were we to give up all distinguishing marks derived from the consideration of these points, since all experience tends to show that a distinction must be drawn between processes of protoplasm thrust forth by vital movement, and capable of being again withdrawn, and the fixed outgrowth of cells. The genetic connection existing between the various kinds of cells found in connective tissue, their physiological peculiarities, the chemical and physical alterations which they undergo from their first origin to a certain period of their life, etc., are all questions which require further investigation.

Lastly, The *pigment cells* of connective tissue require to be specially mentioned. In Man and the higher Vertebrata they occur only in a few limited spots, but they are much more widely distributed in Amphibia and Fishes, appearing especially in the skin, in the serous membranes, and in the tunica adventitia of the vessels.

In these places the pigment may also be found deposited in the form of granules which differ both in shape and color.

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* Langhans, *loc. cit.* Grussendorf, *Zeitschrift für Rationelle Medicin*, 3 R., Bd. xxiv., p. 186.

The pigment cells of connective tissue are for the most part characterized by their beautiful stellate form, and by their numerous processes.

In man, in whom such pigment cells occur normally only in the eye, the pigment granules are of black or brown color. The substance of which they are composed, and which is termed Melanin, is still but little known in regard to its chemical qualities. The granules are not perfectly round, but sub-cylindrical, or elongated with rounded extremities. They more or less completely fill the interior of the stellate pigment cells of the eye. As a general rule the ends of the cell processes remain colorless. The nucleus of these cells, in some cases, occupies the middle of the cell, and appears bright and distinctly defined; it contains no pigment, as is also the case with the cell substance which bridges over the broad side of the nucleus, whilst the cell mass lying around the nucleus, and its processes, are closely packed with the pigment molecules, so that the position of the nucleus appears as a clear space. In the stellate cells of the iris, and of the choroid of man, the pigment granules are most abundant shortly after birth.* Pigment cells also occur in the innermost layer of the sclerotic. In many animals, isolated pigment cells are thickly disseminated throughout the whole thickness of the sclerotic. Movements have been observed in the stellate pigment cells (chromatophores) of Amphibia,† and Fishes.‡ The pigment granules sometimes appear collected into round masses, and at others are diffused in the cell processes, which are often prolonged to a considerable distance. The movements observed are exceedingly tardy in adult frogs, but in the embryos of these Batrachians they are somewhat more active.§ The spontaneous changes of form of the pigment cells in the skin of these animals, or those which are called forth by changes in the intensity of the light, are connected with the phenomena of change of color which they present.‖ Von Wittich¶ has described the effects of electrical excitation of the pigment cells of Hyla arborea, which appear to be most sensitive to it.

In adult specimens of Rana esculenta and temporaria, and also in Tritons, notwithstanding repeated trials, I was unable to perceive that any influence was exerted on the pigment cells by the action of induction shocks of electricity. R. Wagner has observed the presence of stellate pigment cells possessing extraordinary motility in Cephalopods.

THE VARIETIES OF CONNECTIVE TISSUE.—In its first formation, and during the earliest stages of its development, connective tissue consists of cells which, for the most part, lie closely compressed together; it then presents a parenchymatous appearance, similar to that observed in the embryonic tissue of certain neoplastic formations, as the small-celled sarcoma of Virchow.**

Apart from this form of connective tissue, to which we shall again refer in the history of its development, that of the adult organism can be arranged under two heads; one of which includes those varieties of networks and trabeculæ that are developed from cells, whilst the other includes the fibrillar connective tissue, characterized by the presence of peculiar invariably

* Brücke, *Anatomische Beschreibung des menschlichen Augapfels.* Berlin, 1846, p. 20.
† Brücke, *Denkschriften der Wiener Akademie*, Bd. iv., p. 23.
‡ Buchholtz, Reichert and Du Bois' *Archiv*, 1863, p. 74.
§ Büsch, Müller's *Archiv*, 1856, p. 425.
‖ Brücke, *loc. cit.*
¶ Von Wittich, Müller's *Archiv*, 1854, p. 41.
** *Die krankhaften Geschwülste*, Bd. ii., p. 224, fig. 140.

unbranched fibres (connective tissue fibrils) composed of a gelatine-yielding substance.

Connective-tissue Plexuses and Trabeculæ.—These forms do not yield gelatine on boiling. They either occur in large independent masses, or they contain other tissues, to which they give support and covering, in the lacunæ of their meshes, which are sometimes more delicate and sometimes coarser.

a. In the former case the connective tissue is usually characterized by its succulency and its ready compressibility. The larger masses are transparent, or at least very translucent, and on section, in consequence of the escape of fluid, easily collapse (gelatinous tissue of Virchow). On the addition of acetic acid, a flocculent and threadlike precipitate of Mucin can frequently be obtained in considerable quantity from the escaped fluid which is again dissolved on adding an excess of the acid (mucous tissue, Virchow).* The morphological constituents of the tissue consist of delicate and soft cell structures containing nuclei, from which smooth trabeculæ are given off in various directions, that branch and anastomose with one another. Or there may occur in place of the cell plexus a delicate network of smooth non-nucleated trabeculæ, which present enlargements at the points where they intercommunicate. A larger or smaller number of amœboid cells are discoverable in the amorphous substance lying between the fully developed cells.

The tissue of the jelly-like substance of the umbilical cord described by Wharton, as it appears in the earlier periods of the development of the embryo, is to be reckoned amongst these forms. At a later period, especially in preserved specimens, a not inconsiderable quantity of the original tissue may be found, associated sometimes with fasciculi of fibrils, agreeing with those that, as we shall subsequently see, compose the fibrillæ of connective tissue.† The substance which occupies the Sinus rhomboidalis of birds is usually regarded as belonging to the mucous or gelatinous form of connective tissue; and a similar material is frequently met with in fishes, especially in the electric and pseud-electric organs; in the vicinity of the mucous canals of the Sturgeon and Plagiostomata, in various parts of the body in the Carp, Tench, Dace, and Eel, and beneath the sclerotic.‡ The vitreous humor of the eye may also be regarded as an example of it. The presence of gelatinous tissue has also been demonstrated in the Invertebrata, Heteropods, Medusæ, etc.§

As long as we consider a given object to belong to this kind of connective tissue from its external appearance alone, and without regard to its chemical and physiological characters, it is difficult to meet the objection that our generalization is founded on comparatively coarse analogies, which could no longer be maintained were the tissues to be subjected to more accurate chemical and physiological investigation. It may, on the other hand, however, be remarked that a considerable quantity of the connective tissue in the body at a particular stage of its development presents the appearance of gela-

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* *Würzburger Verhandlungen*, Band ii., p. 160, *Cellular Pathologie.*

† Henle, *Jahresbericht für* 1858, p. 61, *et seq.* Weismann, *Zeitschrift für Rationelle Medicin*, Band xi., 3 R., p. 140. Beale, *Structure of the Simple Tissues.* Koster, *Ueber die feinere Structur der menschlich. Nabelschnur* ("On the finer Structure of the Umbilical Cord"), *Inaug. dissert.* Würzburg, 1868, pp. 16 and 17.

‡ Leydig, Müller's *Archiv*, 1854, p. 316.

§ Gegenbaur, *Monographie der Pteropoden und Heteropoden.* Leipzig, 1855. Max Schultze, Müller's *Archiv*, 1856, p. 314. Leydig, *Vergleichende Histologie.* Kölliker, *Zeitschrift für wissenschaftliche Zoologie*, Band iv., p. 363; and *Würzburger Naturw. Zeitschrift*, Band v., p. 232, 1864.

tinous tissue, and also that in pathological neoplastic formations proceeding from connective tissue the same condition is frequently met with.

b. A very delicate retiform connective tissue, fulfilling the purposes of support and protection, and therefore here first mentioned amongst those possessing similar characters, occurs in the connective tissue of the eye and in the interior of the nervous centres (Neuroglia, Virchow). That this is really a form of connective tissue was first maintained by Max Schultze,* with whom Kölliker,† Virchow,‡ Deiters,§ and others are in accordance. In regard to the particular features presented by this form, we must refer to the special descriptions of the several organs. Hirzel and Frey‖ consider they have met the same tissue in the hybernating glands of some mammals.

c. A remarkable form of connective tissue occurs in the supporting and investing reticulum of the glands of the lymphatic system and allied organs in connection with their blood capillaries, and around the fasciculi of fibrillar connective tissue.

In the lymph glands and analogous structures—such as the glands of Peyer, the solitary glands of the intestine, the mucous membrane itself of the alimentary canal, the tonsils, the follicles at the root of the tongue, the trachoma glands of the conjunctiva, the tissue of the conjunctiva itself, and the nasal portion of the pharynx in man—this retiform tissue has been accurately described by Billroth,¶ Eckhard,** Heidenhain,†† His,‡‡ Frey,§§ Henle,‖‖ Stieda,¶¶ and Luschka.*** The meshes of the network are in all these instances filled with cells resembling those of the lymph in various stages of development. The network and the lymphoid cellular elements have been collectively designated adenoid tissue by His, and cytogenous connective tissue by Kölliker. The trabeculæ of the reticulum may be observed also to traverse the larger cavities of these glandular structures.

In the fresh condition, the reticulum is soft and easily torn. It can only be exhibited in its integrity by carefully brushing fine sections of the hardened tissue with a camel-hair pencil (His), by which means the adhering lymphoid cells can be removed. A delicate network remains behind, composed of nucleated cells which enclose rounded or polygonal areolæ. The trabeculæ of this network proceed from a substance surrounding, and somewhat thicker than the nucleus, which may be regarded as the body of one of the stellate cells from which the trabeculæ are derived. The trabeculæ to which such a cell may be referred as a nodal point, or common point of

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* *De Retinæ Structura Penitiori*, Bonn, 1859. *Archiv für Mikroskop. Anatomie*, Band ii., p. 261.

† *Gewebelehre.* Leipzig, 1867, p. 266.

‡ *Die krankhaften Geschwülste*, Band ii., p. 128.

§ *Untersuchungen über Gehirn und Rückenmark, herausgegeben von* Max Schultze. Braunschweig, 1865, p. 27.

‖ Frey, *Histologie und Histochemie*, Leipzig, 1867, p. 233; *und Zeitschrift für wissenschaftliche Zoologie*, Band xii., p. 165.

¶ Müller's *Archiv.* 1857, p. 88, v. *Beiträge zur Pathologischen Histologie*, "Essays on Pathological Histology." Berlin, 1858, p. 126. Virchow's *Archiv*, Band xx., p. 409; and Band xxiii., p. 457. *Zeitschrift für wissenschaftliche Zoologie*, Band xi., p. 325.

** *De glandularum Lymphaticarum Structura.* Berlin, 1858.

†† Reichert and Du Bois' *Archiv*, 1859, p. 460.

‡‡ *Zeitschrift für wissenschaftliche Zoologie*, Band x., p. 333, v. Band xi., p. 416.

§§ *Untersuchungen über die Lymphdrüsen des Menschen und der Säugethiere*, "Researches on the Lymphatic Glands of Man and Mammals." Leipzig, 1861. *Zeitschrift für wissenschaftliche Zoologie*, Band xii., p. 336, and Band xiii., pp. 1 and 28.

‖‖ *Handbuch der Systematischen Anatomie des Menschen*, Band ii., p. 702.

¶¶ *Archiv für Mikroskopische Anatomie*, Band iii., p. 360.

*** *Archiv für Mikroskopische Anatomie*, Band iv., p. 1.

union, are either simple, and join with similar processes given off from neighboring cells, or first give off a series of still finer trabeculæ, which then communicate with each other.

The reticulum of the lymphoid organs contains not only cells in its areolæ, but also supports blood-vessels, and the trabeculæ unite upon the external surface of the vessels to form a kind of Tunica adventitia. And hence in the capillaries, this layer was designated by His the Adventitia capillaris. The trabeculæ of the latter must not be confounded with the processes given off from the wall of the vessel itself, which, as they develop, present in the part lying at some distance from the artery, the appearance of a solid trabecula, but which gradually become hollow as they approximate the artery to which they are attached.

The reticulum does not, in all instances, nor in all parts of the organs above named, present the characters of such a network as we have described. When developed to a greater extent, it passes into a network of non-nucleated trabeculæ* which are of a far more rigid nature, and often appear considerably expanded. A trellis-work of this kind may, from its resistance to acids, easily be mistaken for the elastic fibrous networks we shall hereafter describe, and which have a similar plexiform arrangement. But as the latter are distinguished from the fibrillar connective tissue by the circumstance that the connective tissue fibres are never branched and never form networks, though their fibrous bundles frequently present a net-like arrangement; so is this also distinguished from the elastic fibre networks by the circumstance that, unlike these, it is incapable of resisting the action of a solution of soda. It has been previously stated, that reticula, similar to those found in the lymphatic glands, are found also in other places.

Fig. 12.

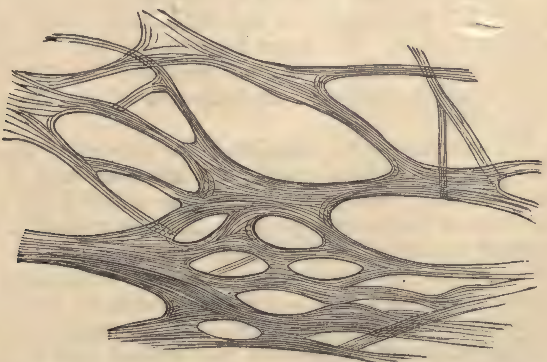

Fig. 12. Trabeculæ from the Ligamentum pectinatum iridis of man.

A wide-meshed network of trabeculæ is found constituting a kind of investing layer, winding around the bundles of the fibrillar connective tissue hereafter to be described. In consequence of the appearances to which this gives rise, when the fasciculi in question swell up under the influence of acetic acid, it has led some to admit the presence of a structureless sheath surrounding each fasciculus. I† have myself depicted and given a descrip-

* Henle, *Zeitschrift für Rationelle Medicin*, Band viii., 3 R., p. 201. Eckhard, *loc. cit.*

† *Wiener Sitzungsberichte*, Band xxx., p. 71, fig. 12.

tion of the spiral trabeculæ found in the skin of the ox. Kölliker,* however, still describes these spiral fibres running around the bundles of the pia mater of the fœtus and recently born animals as a nucleated cell reticulum.

A very delicate investing reticulum developed from nucleated cells (perivascular plexus) has recently been described by Iwanoff † in the vessels of the vitreous humor in the frog. He has also pointed out the distinctions which exist between the trabeculæ of the reticulum and the processes of the vessels.

d. A coarser connective tissue network, with large meshes, composed of broad and stiff trabeculæ, forming a firm homogeneous mass, occurs in the Ligamentum pectinatum iridis of man. These trabeculæ exhibit an indistinct, interrupted, and not very regular longitudinal striation (fig. 12). Max Schultze has well compared them with the anastomosing fibrous cords of the gelatinous substance composing the Medusæ.‡ The statement made by Haase,§ that the Ligamentum pectinatum of man really consists of the fibrillar form of connective tissue, is erroneous.

On the other hand, the Ligamentum pectinatum of animals (ox, sheep, pig), differs from that of man in being composed of connective tissue, with which many elastic fibres are intermingled. The gradual modification the trabeculæ of the Ligamentum pectinatum undergo at the point where they become continuous with the membrane of Descemet in man, is worthy of particular remark, as it can be clearly seen to occur, especially in new-born infants. The trabeculæ widen out; the meshes diminish in diameter, and, near the membrane of the vitreous humor, only present small interstices. In human embryos of about the fifth month, the Ligamentum pectinatum can be still seen to be composed of cells which give off broad processes, communicating with one another in the same way that the trabeculæ do at a later period. In some of these cells the nucleus, which subsequently vanishes, is already small, dull in appearance, and ill-defined, though in others it is still granular and distinct. The latter features are well brought out in preparations colored with carmine. A great number of beautifully defined stellate cells occupy the interspaces of the trabeculæ of the Ligamentum pectinatum just described.

e. There still remains to be mentioned the connective tissue supporting masses which occur in various places, and are composed of fusiform and stellate cells. The best example we can adduce of this is the connective tissue in the interior of the kidneys.‖ This does not present any proper reticulum comparable to that of the previously described forms. In sections of the organ from which the gland tubes have been removed by pencilling, a connective tissue meshwork can indeed be exhibited; but it may also be seen that its trabeculæ form a laminated mass, supporting or investing the tubuli of the gland, in which fusiform and stellate cells lie closely congregated together. Boll¶ has recently described and represented a plexiform connective tissue, consisting of a simple layer of cells united into a plexus, investing the acini of the salivary and lachrymal glands.

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* *Zeitschrift für wissenschaftliche Zoologie*, Band ix., p. 146; *und Gewebelehre.* Leipzig, 1867, p. 79, fig. 36.

† *Centralblatt für die Medicinischen Wissenschaften*, 1868, No. 9.

‡ Muller's *Archiv*, 1856, p. 319, fig. 7.

§ *Archiv für Ophthalmologie*. Band xiv., p. 48, *et seq.*

‖ *A. Beer, die Bindesubstanz der menschlichen Niere*, etc., "The Connective Tissue of the Human Kidney," etc. Berlin, 1859. Isaac's *Recherches sur la Structure et la Physiologie du Rein, Journal de la Physiologie*, T. i. Paris, 1858, p. 577. Kölliker, *Handbuch der Gewebelehre.* Leipzig, 1866, p. 509.

¶ *Archiv für Mikroskopische Anatomie*, Band iv., p. 146, T. i.

An investing layer of fusiform cells constituting a perineurium may be found also on the peripheric branches of nerves, especially amongst the Batrachia.

A similar covering is also found in the excretory ducts of the mammary glands and elsewhere.

The forms of connective tissue hitherto described are distinct from the fibrillar connective tissue which is so frequently found in the adult organism. In this, the connective tissue fibrils, which are so well characterized by their yielding gelatine on boiling, by their unbranched course, their smooth edges, and equal thickness, constitute the essential morphological constituent. It must be admitted, however, that in certain cases transitional forms occur between the fibrillar and the above-mentioned forms of connective tissue. These may be met with in many places, but clearly do not hinder us from admitting that in other places a distinction may be drawn between the two in accordance with the facts already given. Otherwise, the difficulty may easily arise that was frequently observable in the old discussion, as to whether the structures under examination should be regarded as connective or as elastic tissue.

Fibrillar Connective Tissue.—This is the most widely distributed form that is found amongst the Vertebrata; but it has not been clearly proved whether it occurs amongst the Invertebrata. The connective tissue which is most similar to the fibrillar connective tissue of Vertebrata is that described by Leydig in the Cephalopods.* According to the same inquirer,† a fibrillar connective tissue, very similar to fibrous connective tissue, occurs also in the Echinodermata. Reichert described as belonging to connective tissue, certain tissues found in Arthropods, Molluscs, and Vermes. No evidence, however, is furnished, that these tissues are gelatine-yielding.

Fig. 13.

Fig. 13. Tendon of man, showing fibrils and fusiform cells.

Several of them probably consist rather of Chitin. Schlossberger‡ obtained no gelatine from the claws of crabs.

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* Muller's *Archiv*, 1854, pp. 303 and 310.
† *Loc. cit.*
‡ *Chemie der Gewebe. Leipzig und Heidelberg*, 1856, p. 300.

Originally, fibrillar connective tissue, as already mentioned, was the only form to which the term connective tissue was applied. The morphological constituents which can be demonstrated in it, are fibres and cells of various kinds. These elements are only here and there in direct contact with each other; elsewhere the intervening spaces are occupied with a material of variable consistence.

In the fibrillar connective tissue of adult animals a certain kind of the fibrous elementary form constitutes so large a proportion of the old tissue that it exclusively occupied the attention of the earlier investigators. This is composed of the already frequently mentioned gelatine-yielding fibril. The simplest preparation, the mere teasing out with needles of a small portion of fibrillar connective tissue, shows that it may be split into skein-like portions of various breadth.

The lateral borders of these cords present straight or more or less sinuous outlines; and with strong magnifying powers fine striæ may be observed lying in close contiguity to one another, and following accurately, in a longitudinal direction, the contour of the cord. In thin transparent membranes, as, for example, in the mesentery, or in the arachnoid, these fasciculi of the connective tissue may be immediately recognized without any preparation. If such longitudinally striated cords be further broken up, we may easily convince ourselves that, in accordance with the longitudinal striation they exhibit (fig. 13), they may be split into fine smooth fibres, running for considerable distances without apparently giving off any branches. The diameter of these fibres is very small, varying from 0·0006 to 0·002 millimetres. These fibres are the fibrillæ of the connective tissue; and when examined by means of the polarizing microscope, the fibrils and the fasciculi they form prove to be doubly refractile.* The axis lies in the longitudinal direction of the fibrils, and they behave as positive uniaxial crystals.† They cannot, however, be isolated from the connective tissue by simple mechanical means. We possess, however, in solutions of lime and baryta, fluids which, if they have acted for some time upon connective tissue, loosen the adhesion of the fibres to one another to so great an extent that nothing further is required to obtain the detached fasciculi and even completely isolated fibres for microscopical investigation. The lime-water in which connective tissue, freed as far as possible from extraneous substances (*e. g.*, clean tendon), has undergone this loosening of its cohesion, contains a substance which can be precipitated from it by means of acetic acid in the form of white granules, which subsequently form flocculi. This reaction still occurs, even if the connective tissue, before being placed in the lime-water, has had all the albuminous substances soluble in water as far as possible withdrawn from it. The substance taken up by the lime-water, and capable of being again precipitated from it, agrees in its reactions with Mucin.‡ On account of the mechanical alteration which the connective tissue fibrils undergo by this procedure, it may reasonably be admitted that a solution has taken place of a cementing substance occupying the interspaces between, and binding together, the fibrous elements.§ Wherever the fasciculi of the

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* Erlach, Müller's *Archiv*, 1847, p. 322.

† W. Müller, *Zeitschrift für Rationelle Medicin*, 3 R., Band x., p. 173. See also Valentin, *Untersuchung der Pflanzen, und Thiergewebe im polarisirten Lichte*, p. 265, "Researches on the Tissues of Plants and Animals in Polarized Light;" and Mattenheimer, Reichert and Du Bois' *Archiv*, 1860, p. 354.

‡ Rollett, *Sitzungsberichte der Wiener Akademie*, Band xxxix., p. 308. Eichwald, *Annalen der Chemie und Pharmacie*, Band cxxxiv., p. 177.

§ Rollett, *Sitzungsberichte der Wiener Akademie*, Band xxx., p. 43.

connective tissue appear separated to a considerable distance from one another, an intervening material of this kind may be directly observed. Statements in accordance with this were first made by Schwann, and subsequently by Henle, the meshes of the arachnoid being particularly alluded to by the last-named author.*

Kühne † demonstrates the possession of quite definite mechanical peculiarities by the homogeneous substance intervening between the muscles of the frog which only contains scattered fibrils. A separation of connective tissue into fibrils can also be attained through the chemical action of permanganate of potash.‡ Connective tissue, when acted on by permanganate of potash, becomes stained of a brown color; and if it be then treated with boiling nitric acid and ammonia, it no longer assumes a yellow color. Connective tissue that has been well washed,§ furnishes only feeble indications of the xantho-proteinic acid reaction.‖ The same occurs with tendons that have undergone calcification. It thus appears that it is not the collagenous substance which causes all insufficiently purified connective tissue to become stained yellow with these reagents.¶ The fibrils of the connective tissue, and the fasciculi which they form, undergo a peculiar change at a high temperature. When placed in boiling water, they rapidly contract, becoming shorter but much thicker than in the fresh condition, and at the same time presenting a much more delicate outline. Coincidently the characteristic longitudinal striation of the fasciculi is lost. These, equally with the compact connective tissue in which coarse fasciculi lie in intimate connection with one another, assume the appearance of a homogeneous mass, in which, however, under the microscope, various deposits that scarcely appear in the fresh tissue, or altogether escape notice, are clearly brought into view.

The sudden shrivelling which the fibrils of connective tissue undergo in boiling water, depends on a peculiar molecular metamorphosis of the substance of the fibrils. It is impossible to demonstrate that any imbibition of water occurs. If the connective tissue be exposed to a boiling temperature, whilst at the same time any shortening in the longitudinal direction of the fibres is prevented, the tissue thus heated, when dried, still retains, under the microscope, its fascicular and fibrous character. If small portions of tendon are macerated in water of various temperature, it will be observed that sudden contraction occurs at as low a temperature as between 140° and 158° Fahr. When connective tissue is long subjected to a boiling temperature, or is placed for a shorter time in a Papin's digester, or if, in its natural condition of moisture, it is heated in a test tube to 248° Fahr.,** it dissolves away in the manner already mentioned, and the fibres can in this mode be isolated. The solutions which are obtained usually contain gelatine or "Glutin."

On account of their property of yielding gelatine on boiling, the fibrils and fasciculi of connective tissue are termed collagenous substance. The conversion into gelatine occurs even at 104° Fahr., providing dilute acids

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* Henle, *Allgemeine Anatomie*, p. 349.

† Kuhne, *Lehrbuch der Physiologischen Chemie.* Leipzig. 1866, p. 359.

‡ Rollett, *Sitzungsberichte der Wiener Akademie,* Band xxxiii., p. 519, *et seq.*

§ Rollett, *loc. cit.*, Band xxxiii., p. 523.

‖ Donders, *Holländische Beiträge*, Band i., 1848, p. 67.

¶ Paulsen, *Observationes Microchemicæ.* Mitau, 1849.

** Rollett, Kühne, *Ueber die peripherischen Endorgane der motorischen Nerven*, p. 6. Leipzig, 1862.

have been added; as, for example, sulphurous acid,* or 0·1 per cent. of sulphuric acid.† Founded on these facts, methods have been suggested for the isolation of microscopic structures which do not yield gelatine, but which are imbedded in or surrounded by connective tissue. The first effect of the acid, when applied at ordinary temperatures, is that the tissue swells up to a great extent, especially in the direction of the transverse diameter of the fasciculi and fibrils. The latter, which are thus rendered less strongly refractile, become so compressed against one another with their glutinous surfaces, that their contours can no longer be distinguished; and in the transparent mass, as in boiled connective tissue, new elementary forms now make their appearance. Acetic acid is usually employed to produce this change, and by this means to distinguish the fibrils of connective tissue from those of other fibrous structures.

Several other vegetable acids and diluted mineral acids, especially hydrochloric acid of 0·1 per cent., and similarly diluted nitric acid, act in the same manner as acetic acid.

After treatment with acids, contractions resembling an hour-glass frequently occur in the fasciculi of connective tissue, their enlargement appearing to be prevented at certain points by a firmly applied ligature. These are the much-discussed fasciculi of connective tissue surrounded by coiled fibres. The appearance of constrictions was formerly held to be due to spiral fibres winding round the fasciculi, which, on account of their not swelling in acetic acid, were considered to be of an elastic nature.‡

At a later period attempts were made in various quarters to support a view first advanced by Reichert,§ which attributed the contractions of the swollen bundles to the sheath of the connective tissue being torn in the act of swelling up into loop-like portions. The presence of such a sheath covering the fasciculi in the form of a continuous membrane cannot, however, be demonstrated in fresh fasciculi; we may, however, convince ourselves of the presence of coiled fibres forming a plexus around these, the fibres being sometimes finer and sometimes coarser. On the cautious addition of alkalies to connective tissue swollen by means of acids till neutralization is effected, it may again be made to resume its original appearance; a fact which Henle first adduced against Reichert's view, who especially rested his doctrine upon the absence of apparent structure in the fibrillar connective tissue when acted on by acetic acid, and on the impossibility of splitting connective tissue into fibres otherwise than by mechanical means. The proposition of Reichert is also negatived by the facts already adduced.

In reference to the capability of bringing back the fibrils and bundles to their original condition after having been swollen by immersion in acids, it must be remarked that the experiment must not be too long delayed, since protracted action of acids, even at a low temperature, actually effects the solution of the fibrils with formation of gelatine. It is further to be remarked that, in solutions of pure alkalies, connective tissue in the first instance swells up into the form of a transparent jelly, and that at a later period the fibrils undergo complete solution. Concentrated nitric acid, at the commencement of its action, causes the same sudden contraction of the fibres of connective tissue that occurs at temperatures exceeding 140° Fahr.

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* Ruthay, *Annalen der Chemie und Pharmacie*, Band xli., p. 236.

† Kühne, *loc. cit.*, p. 11.

‡ Henle, *Allgemeine Anatomie*, Band cxcv., *Jahresbericht für* 1857, p. 38.

§ Reichert, Müller's *Archiv*, 1847. Leydig, *Histologie des Menschen und der Thiere.* Frankfurt, 1857, p. 31. Klopsch, Müller's *Archiv*, 1858, p. 417. Kölliker, *Zeitschrift für wissenschaftliche Zoologie*, Band ix., p. 140.

When covered with chloride of calcium or potash, the fascicula and fibrils become hardened by the withdrawal of water. In solutions of tannin a sufficient quantity of connective tissue soon removes all the acid. Leather thus obtained, especially if the connective tissue have previously been exposed to the action of lime, is better adapted than when hardened by other means, for the preparation of fine sections, to exhibit the arrangement of the fasciculi in compact masses.*

If in such sections the fasciculi, hitherto only considered in the direction of their length, be cut across, the fine transverse sections of the fibrils lying in close contiguity with one another appear in the form of round or somewhat angular dots. This view is, however, far better obtained if the fresh tissue be allowed to freeze on a leaden plate, resting on an iron support, and so imbedded in a freezing mixture that only the upper surface is exposed, the sections being then made on the plate with a cold knife. Henle and Stadelmann † were the first to see the transverse sections of the fibrils in sections of dry tendon.

Sections made from frozen or dry tendons, when treated with acetic acid, are so acted on that the edges of the divided fasciculi curl up, as a con-

Fig. 14.

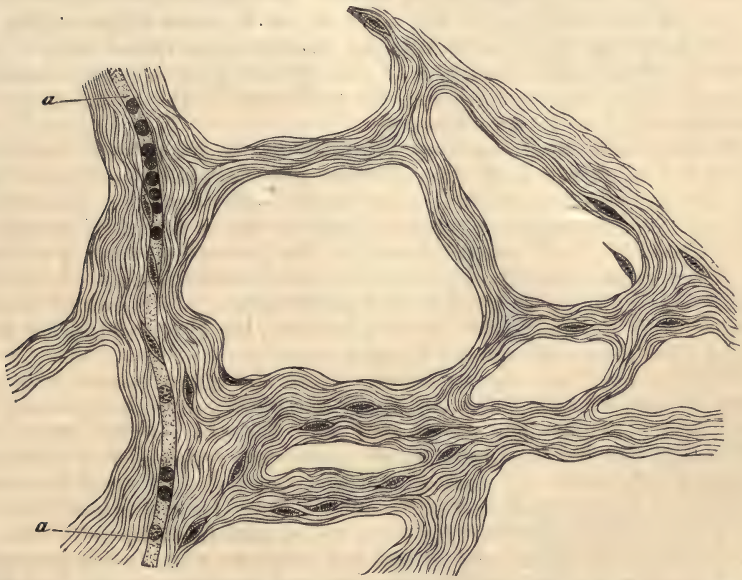

Fig. 14. Fibrillar connective tissue from Peritoneum of man. *a a*, a blood-vessel.

sequence apparently of the rapid swelling that takes place in the direction of their transverse diameter. A peculiar appearance is thus presented, which was first described by Donders,‡ and more recently by Gerlach § and

* Rollett, *Sitzungsberichte der Wiener Akademie*, Band xxx., p. 45, fig. 3, Taf. 1.
† *Sectiones transversæ*, etc., *Diss. inaug.*, 1844; Henle's *Jahresbericht*, 1844, p. 15.
‡ *Holländische Beiträge*, Band i., p. 258.
§ *Handbuch der Gewebelehre.* Mainz, 1850, p. 110, fig. 42.

Machik.* The involuted edges cross each other in the form of broad bands with transversely striated surfaces and sinuous borders.

The fibrils and fasciculi of fibrils of connective tissue are differently disposed in different instances.† The fasciculi may either run parallel to one another, or unite at very acute angles, as in tendons and ligaments; or the variously sized fasciculi, as they decussate at different angles, may divide and again unite to form a thicker or thinner felt-like layer, through which three sections perpendicular to each other may be so carried as that one may strike all the bundles principally in the longitudinal direction, whilst the other two present fibres running in an oblique and transverse direction. In either of the two latter sections the fasciculi may run chiefly in one or other direction, and thus transitional forms may originate, passing into a parallel arrangement. The modes of arrangement above described are found principally in the skin and other membranes composed of connective tissue.

A peculiar arrangement of the fasciculi occurs in the serous membranes, and is most beautifully displayed in the peritoneum of man (fig. 14) and many mammals. The fasciculi of fibrils coursing in this thin membrane, by their frequent division and reunion, have larger or smaller interstices between them, so that the whole membrane presents a gauzy appearance. A very important character to be noticed here is, that the borders of the interstices contain loops of fibrils which appear to round off the angles.

The foregoing arrangement has been described as a special form of connective tissue, under the name of the retiform,‡ or areolar connective tissue.§ These expressions, however, refer only to the peculiar appearances presented under the microscope.

Another mode of arrangement exhibited by the fasciculi of connective tissue is that in which, of three sections made perpendicularly to one another, none of the fibrous bundles run chiefly longitudinally or transversely, but each section presents bundles running in the most various directions. This form occurs, but not exclusively, in the interstitial connective tissue of various organs, as well as in the amorphous connective tissue of Henle,‖ whilst the kinds previously described preponderate in the formed connective tissue of Henle. Henle himself, however, has not attempted to draw a very sharp line of distinction between them.

Differences between the connective tissue of different organs not only occur in regard to the arrangement of the fasciculi, as we have already remarked, but the fasciculi themselves show varieties, so that in certain organs the fine fibrils appear in all transverse sections of a fasciculus arranged parallel to one another, and at equal and very small distances, resembling the straight or slightly sinuous edge of a fasciculus, whilst in other instances the fibrils are collected into smaller fasciculi, the borders of which present very close undulations, and which are more loosely arranged. On this account, when treated with lime and baryta-water, the first kind of fasciculi immediately splits into fibrils, whilst the second divides in the first instance into sections, and these again break up into fibrils.

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* *Sitzungsberichte der Wiener Akademie*, Band xxxiv., p. 91.

† Bruch, *Zeitschrift für Rationelle Medicin*, Band vii., pp. 378 and 379. Leydig, *Histologie des Menschen und der Thiere.* Frankfurt, p. 79. Rollett, *Sitzungsberichte der Wiener Akademie*, Band xxx., p. 45, *et seq.*

‡ Kölliker, *Gewebelehre.* Leipzig, 1867, p. 74.

§ Hassall, *Mikroskopische Anatomie*, translated by Kohlschütter. Leipzig, 1852, p. 232, Taf. 35, fig. 7.

‖ *Allgemeine Anatomie*, p. 354.

I have already elsewhere observed * that these differences are most clearly discernible on making a comparative examination of the sclerotic and conjunctiva of the same eye.

Fasciculi of the former kind occur in the tissues that were formerly called fibrous. Fasciculi of the latter kind in ordinary connective tissue.

A few remarks may here be made in regard to the lacunæ or interstices of connective tissue.

It is impossible for any one who has carefully examined the structure of this tissue to doubt that interfibrillar fissures occur in it. It is also extremely easy to perceive that the collagenous substance is not in equally intimate contact in all parts of a given portion, or, in other words, that it does not everywhere cohere with equal firmness. The varieties in the arrangement of the fibrils and of the fasciculi, and the results of the disintegration which occurs with lime and baryta-water, also clearly prove this, especially in those forms of connective tissue where the above-mentioned coiled or ring-like arrangement of fibres around the fasciculi is absent.

It cannot therefore be maintained that the fibrils and fasciculi swim in a fluid equally distributed amongst them, as Engelmann † holds to be the case in the cornea, nor can we admit with His ‡ that the mucous or mucoid substance, nor the above-mentioned cementing material, is quite equally distributed between the fibrils and fasciculi. The experiments made by Von Wittich,§ in which he endeavored to demonstrate experimentally the existence of the plasmatic canal system of Virchow, by allowing tendons to absorb particles of indigo through the action of capillarity, and in which he found a finely divided blue precipitate in the tendons, do indeed speak in favor of this view. It is impossible, however, to prove by such means that the passages between the firmly united fasciculi and fibrils can be represented in the form of a canal system communicating with the origins of the lymphatic capillaries, analogous to that described by Von Recklinghausen ‖ under the name of serous canals, from the appearances presented after treatment with nitrate of silver. These questions will be discussed in the section on the lymphatic system. It must be acknowledged, however, in regard to the migrating cells of this form of tissue considered generally, that they cannot enter it at any point indiscriminately, but only through determinate passages, resulting not only from the impermeability of the collagenous substance, but also from the unequal distribution of the firmer cementing substance.

The mode in which the cells of the fibrillar tissue can best be represented and investigated has already been given. If we have pursued this plan with tissue in as fresh a condition as possible, it will always be found that fibrils and cells are coincidently brought into view (figs. 13 and 14). It may here further be mentioned that very beautiful preparations may be obtained in dense connective tissue by the aid of chloride of gold, after the action of which the cells appear red or bluish red, whilst the fibrous material remains uncolored.¶ Formerly, acetic acid was frequently employed to bring the cells of connective tissue into view; but on account of the

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* *Loc. cit.*, p. 58.

† *Ueber die Hornhaut des Auges*, "On the Cornea." Leipzig, 1867, p 6.

‡ *Die Häute und Höhlen des Körpers*, "The Membranes and Cavities of the Body." Basel, 1865, p. 23.

§ Virchow's *Archiv*, Band ix., p. 187.

‖ *Die Lymphgefässe und ihre Beziehung zum Bindegewebe*, "The Lymph Vessels, and their relations to Connective Tissue. Berlin, 1862.

¶ Cohnheim, *Archiv für Pathologische Anatomie*, Band xxxviii., p. 352.

changes which this reagent induces in the cells, and the circumstance that the true disposition of fibrils and fasciculi disappear under its influence, the modes of treatment above recommended will be found to be more appropriate.

The subjection of the tissue to a boiling temperature was in like manner formerly recommended; * but, as we now know, this method leads to illusory appearances of the stellate cells brought into view on making transverse section of tendons.† It is also apt to produce erroneous impressions in the case of other organs composed of connective tissue, from the circumstance that the contracted closely compressed fasciculi, where they lie in juxtaposition in the transverse section, present three or four-sided fissures with incurved sides between them.

Besides the cells, sharply defined fibres become apparent in connective tissue either after treatment with acids, or on boiling, as we shall presently describe. Where, however, it is desired to obtain a rapid general view of the disposition of these parts, the last-mentioned method can alone be employed.

THE ELASTIC FIBRES.—These fibres, which are apparent in all forms of connective tissue that have been rendered transparent by treatment with acetic acid or by boiling, are sharply defined, and present smooth edges. In boiled connective tissue they are distinguished by their spiral or coiled course, but in connective tissue swollen by immersion in acid they pursue a somewhat straighter course. These fibres are distinguished from those of the connective tissue, not only by the resistance which they offer to the above-mentioned agents, but also by the circumstance that they present a remarkable tendency to branch and form networks. They are sometimes only sparingly present, and then usually exhibit the form of cylindrical delicate fibrils of about the same size as those of the connective tissue—slightly branched, and forming long large meshes, as in the tendons of man; or, on the other hand, they may be present in greater numbers, may branch repeatedly, and, being connected by frequent anastomoses, form a fine delicate plexus, as on the surface of many serous and mucous membranes. The several fibres may also coalesce to form one of considerable thickness; they may also expand in the form of flattened trabeculæ, which combine with similar or still finer fibres proceeding from the branches of the trabeculæ, to form a very characteristic plexus, as in the cutis and the lungs. In several places, as, for instance, in the ligamentum nuchæ of animals, in the ligamenta subflava of the vertebral column, and in the elastic tissue of the arteries, the elastic fibres exist in such quantity that they are commonly regarded as forming an independent elastic tissue or membrane. The fibres here are for the most part thick, and branch and communicate at more or less acute angles, so that only narrow and elongated, or small round or oval meshes, lie between them. The trabeculæ often appear very much expanded, or become fused together into elastic plates or membranes, which are perforated by sharply defined foramina constituting the so-called fenestrated membrane of the arterial tunics.

The elastic fibres undergo no change from exposure to the action of either dilute or concentrated acetic acid, and they resist for a very long

* Henle, *Jahresbericht*, 1850, p. 40; and Virchow, *Würzburger Verhandlungen*, Band ii., p. 154.

† Henle, *Jahresbericht*, 1851, p. 23. Reichert, Müller's *Archiv*, 1854, p. 38. Bruch, *Zeitschrift für wissenschaftliche Zoologie*, Band vi., p 474. Rollett, *loc. cit.*, Band xxx., p. 69.

period, at ordinary temperature, the action both of potash and soda. The latter forms one of the best means of bringing them into view. Concentrated sulphuric acid makes the elastic fibres clearer without immediately causing them to swell up, and its action requires to be continued for many days before the fibres swell and begin to dissolve. The elastic fibres do not dissolve on boiling, at least in the time requisite to convert the collagen of connective tissue into gelatine; and if connective tissue and albuminoid substances have been removed from the specimen, as, for instance, from the ligamentum nuchæ, by means of solution of potash, no gelatine, in the ordinary sense of the word, can be obtained. It must be admitted, however, that the elastic fibres themselves undergo solution on continuous boiling,* or on exposure to a temperature of 320° Fahr. for thirty hours. By these means, however, only a non-gelatinizing brownish fluid can be obtained, smelling of glue, and precipitable by tannic acid.

Moreover, if connective tissue be converted into gelatine by digestion with acids, at 104° Fahr., the elastic fibres remain unaffected.† The elastic fibres are reddened with Millon's reagent, and give the xantho-proteinic acid reaction. The ligamentum nuchæ, after being purified by successive treatment with alcohol, ether, boiling water, acetic acid, and alkalies, has been described and analyzed by W. Müller‡ under the name of Elastin.

In the elastic fibres of the skin and of the subserous layers of the peritoneum, and of the chordæ tendineæ of the dog, Von Recklinghausen§ saw, after treatment with nitrate of silver, a black precipitate occur here and there in the interior of the fibres, and is hence inclined to regard them as hollow. This appearance does not occur in the fibres of the ligamentum nuchæ, nor in those of the elastic coat of the vessels. Frey‖ believed that he had witnessed a precipitation of carmine granules in the interior of many elastic fibres after maceration in a solution of carmine and ammonia, and subsequent neutralization with acetic acid; but he is doubtful whether the question of the tubular nature of the fibres can be thus decided. Von Wittich¶ obtained no precipitate in the elastic fibres of the ligamentum nuchæ in his experiments with indigo. There is certainly no indication of an internal cavity presented on the examination of the broad transverse sections of the elastic fibres of this ligament.

DISTRIBUTION OF THE FIBRILLAR CONNECTIVE TISSUE IN MAN.—In regard to this point, the parts that consist of fibrillar connective tissue in man are the ligaments of the skeleton, the periosteum, and perichondrium; the aponeuroses, fasciæ, and tendons; the fibrous membranes, the stroma of the serous membranes, of the majority of mucous membranes, and of the skin; and the subserous, subcutaneous, and submucous connective tissues: it occurs also in the tunics of the vessels, especially in the tunica adventitia and in the endocardium, in the vascular membranes of the eye, and of the central nervous apparatus, and as interstitial connective tissue in most organs.

DEVELOPMENT OF CONNECTIVE TISSUE.—The question of the development

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* Eulenburg, *De tela Elastica*, Berlin, 1836; and J. Müller, Poggendorf's *Annalen*, 1836, Band xxxviii., p. 311.

† Kühne, *Physiologische Chemie.* Leipzig, 1866, p. 356.

‡ *Zeitschrift für Rationelle Medicin*, Band x., 3 R., p. 173.

§ *Die Lymphgefässe*, etc., p. 59.

‖ *Histologie und Histochemie.* Leipzig, 1867, p. 247.

¶ *Archiv für Pathologische Anatomie*, Band x., p. 187.

of fibrillar connective tissue is one of the most difficult in the whole range of histological inquiry. After Henle* had opposed the view of Schwann,† that the cells becoming greatly elongated split into the fasciculi of fibrils, the view of the latter constantly gained ground, that an originally homogeneous substance, containing certain constituents, distributed through it subsequently split into fasciculi and fibrils. But the significance attached to the various forms and material here met with by various authors was very different. According to the view of Reichert,‡ the homogeneous substance which subsequently becomes converted into the fasciculi and fibrils, proceeds from the coalescence of cell membranes with an intercellular substance; the fasciculi and fibrils are only the optical expression of a duplicature of this substance, whilst the cells, with their nuclei, or with the exception only of their nuclei, undergo atrophy. According to another explanation, it is not the blastema existing between the nuclei that undergoes conversion into a fibrillar tissue, but the formed elements between which this is so abundant as an intercellular substance, and which are the fusiform cells demonstrated by Schwann in embryonic connective tissue. The latter, again, according to Virchow,§ Donders,‖ and Kölliker,¶ take no share in the fibrillation of the tissue, but persist in a somewhat atrophied condition as cells (Virchow, Kölliker), or become converted into a plasmatic canal system (Virchow), or, lastly, pass through transitional forms into a plexus of elastic fibres (Donders).

Max Schultze** and Beale,†† as has been already stated, and with whom many others agree, consider the matrix which is gradually assuming a fibrillar form, to be the protoplasm of membraneless embryonic cells which have fused with one another, and the remains of which, after the formation of the fibrils, are represented by the nuclei with a little unaltered protoplasm around them, constituting the so-called connective tissue corpuscles.

Very recently, Kusnetzoff‡‡ and Obersteiner§§ have maintained that the fibrils of connective tissue originate immediately from the outgrowth of undivided or branched processes of the cells.

In opposition to these various views we must first fix our attention on those definite forms with which we meet in following out the development of connective tissue through as many stages as possible.

And, in the first place, it must be remarked that the tendons and other more dense connective tissue structures, do not furnish the most appropriate objects for examination. Better specimens are obtained from the thin laminæ of serous membranes which were used by Henle and Baur. The peritoneum of the embryo of man and other animals, preserved in Müller's fluid, constitutes an exceptionally good object for examination.

After removal of the epithelium it will there be seen that the superficial layer consists of roundish or somewhat elongated closely compressed cells. In the embryo of a sheep, measuring an inch and a half, these cells are on

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* *Allgemeine Anatomie*, p. 379.

† *Mikroskopische Untersuchungen über die Uebereinstimmung*, etc. Berlin, 1839, p. 133, *et seq.*

‡ *Beiträge zur vergleichenden Anatomie*, etc., p. 108.

§ *Loc. cit.*

‖ *Loc. cit.*, Band iii., p. 348.

¶ *Neue Untersuchengen über die Entwickelung des Bindegewebes.* Würzburg, 1861. *Gewebelehre.* Leipzig, 1867, p. 76.

** Reichert and Du Bois' *Archiv*, 1861, p. 13.

†† *Loc. cit.*

‡‡ *Sitzungsberichte der Wiener Akademie*, Band lvi., p. 162.

§§ *Idem*, p. 251.

the average 0·0256 in length, and 0·0096 in breadth; their nuclei are round or slightly oval; they have a granular aspect, but the granules possess no peculiar brilliancy, and the whole nucleus is not distinguished from the surrounding protoplasm by any very sharp line of demarcation. The protoplasm of the cell appears faintly clouded without distinct granulation. Where these cells lie in close contiguity, their contour lines either altogether disappear or are but feebly marked. The cells may be obtained in an iso-

Fig. 15.

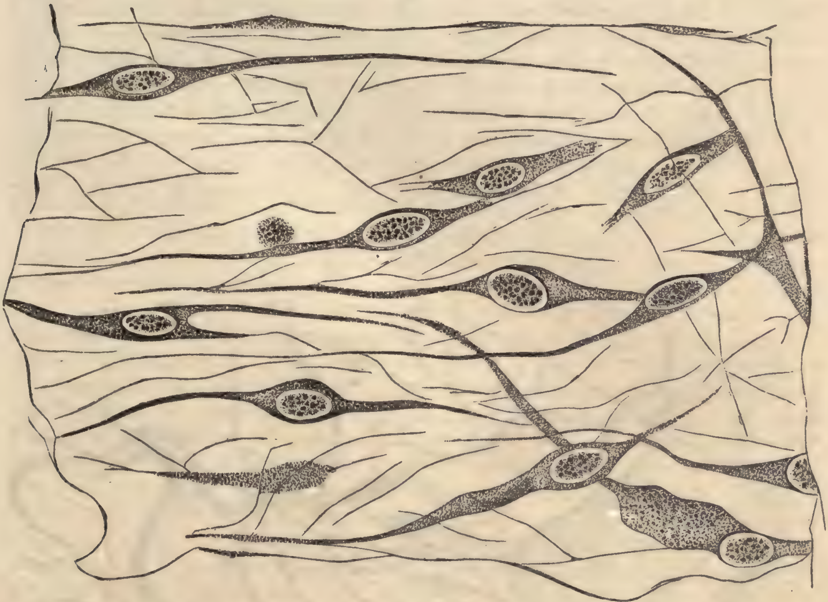

Fig. 15. From the decidua of the embryo of a sheep three inches in length.

lated condition at the edges of the preparation, or on slightly breaking the specimen up with needles.

When these appearances are visible, and they may be rendered much more distinct by staining with carmine, we may easily imagine we have a blastema containing nuclei or coalesced masses of protoplasm, from the cleavage of which the fibrils originate, before us; but this period is still very remote from that at which fibrils make their appearance in the peritoneum. The appearances above described pass immediately into the following.

The nuclei, which in the first instance are ill defined, become vesicular, with distinct double contours at their margins; they are transparent, but contain in their interior a mass of coarse granules elongated in the direction of the longer axis. The cells become attenuated, and assume an elongated spindle shape (fig. 15). The processes are here and there knotted, branch sparingly, and are frequently connected with one another by their extremities. Two enlargements containing nuclei are often only connected together by a short bridge of protoplasm, and with their processes present the appearance of a bi-nucleated double fusiform mass. Fusiform cells divided transversely may also in some instances, though rarely, be seen. These long and beautiful

fusiform cells appear to be widely separated from one another by a clear substance, in which, at an early period, nothing more may be perceived than short interrupted sinuous lines. It is very remarkable that between the above-described elongated cells other round cells are scattered; these exhibit a granular appearance, and one or more nuclei resembling those of the amœboid cells. The formation of these structures may be well followed in the above-mentioned embryos of sheep of from an inch and a half to two inches in length, and here most beautiful examples of the fusiform cells of embryonic connective tissue described by Schwann and Virchow may also be seen. Such fusiform cells occur also abundantly in the peritoneum of older embryos, but during their intra-uterine life they pass their prime. Their processes in particular become attenuated, though they still remain very long, and it requires considerable trouble to follow them out to their termination. It is at this period that the looped smooth unbranched fibrils first appear in small numbers and scattered in the clear matrix between the cells. These, crossing the cell processes at various angles, may be followed over an entire series of fusiform cells; in many instances, however, they

Fig. 16.

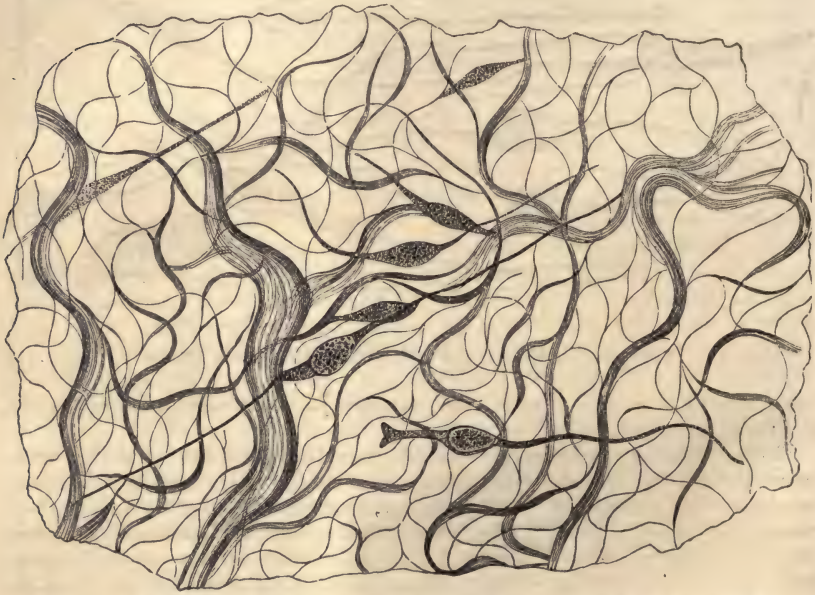

Fig. 16. From the peritoneum of a human embryo of the age of five months.

attach themselves for a short distance to the long axis of the fusiform cells, and appearances are then produced which may easily lead to the idea of a connection between the fibrils and the cells. But there are many other appearances by which we may convince ourselves that such a connection between the very finely pointed cell processes and the equally fine fibrils does not exist. By commencing at the cells, and using proper precautions, their long processes may be followed quite to their extremity with a No. 10 immersion lens of Hartnack; on the other hand, the individual fibrils may be equally well followed throughout the entire preparation, and over all the cells

continuously, in the form of smooth, slightly sinuous, but never thickened threads. The substance of the cell processes becomes somewhat more strongly colored with carmine than the fibrils; their border, however, has not so smooth an appearance, but exhibits very fine irregularities, and is at short distances slightly varicose and somewhat angularly bent.

At the time when the fibrillæ make their appearance the connective tissue of the peritoneum forms a continuous lamella, remaining in this condition until, in addition to several looped fibrils, fasciculi have also become developed. The peritoneum of a human embryo at the fifth month permits a very clear view to be obtained of the fascicular fibrils and fine elongated fusiform cells (fig. 16).

At a later period, however, there appear in man and certain animals—for example, in the dog, but not in the sheep—larger or smaller sharply defined foramina.* In human infants these are much less numerous and much smaller than in adults, and the fine striæ of the surrounding fibrils may be here observed running close to the margin of each foramen.

If the process of development be further followed, as I have done in the peritoneum of a child of one year old, and from thence up to the eleventh year, we may observe that the number of the foramina in the membrane undergoes continuous increase, and the fasciculi and bundles of fibrils augment in thickness, which may be particularly well seen in the fibres surrounding the foramina. It certainly cannot be observed during this growth of the membrane that the fibrils originate from the processes of the cells.

If we pass from the examination of the peritoneum to the tendons of embryos, treated in a similar manner, much caution must be used in drawing conclusions respecting the appearances presented.

In young embryos, closely compressed roundish formative cells may be found at an early period, containing as yet only imperfectly differentiated nuclei. Such cells become, to some extent, elongated in the direction of the long axis of the tendon, and their margins are not very well defined. The isolated cells present the appearance of delicate flocculi in carmine preparations, with the deeply reddened nucleus in their centre. These cells subsequently increase in point of length, as do also their nuclei, the latter becoming at the same time more sharply defined, clear at their margins, and presenting an elongated mass of granules in their interior. The elongated cells appear to be composed of a more strongly refractile substance than the primitive cells, and are capable of being more easily isolated. A clear, smooth intervening substance similar to that which precedes the conversion of connective tissue into plexuses of fibrils, is not here visible; on the contrary, we constantly meet with fine, smooth, completely homogeneous and transparent fibrils, which at first are only few in number, but are subsequently more numerous, lying between the cells which have then become elongated, better defined, and more attenuated. The fibrils can be easily isolated by teasing out the tissue, providing the cells have not become very much elongated, and they may also frequently be followed without interruption over the whole extent of the portion of tendon under observation. If the cells have become elongated, and they undergo lengthening both in an absolute sense, as well as relatively to their breadth—their breadth, indeed, becoming absolutely less—the number of the fibrils undergoes a considerable increase. These, again, may be followed uninterruptedly through the entire tendon, as well as over a whole series of cells. Lastly, amongst a large number of

* See Bruch, *Zeitschrift für Rationelle Medicin*, Band viii., fig. 1.

recently formed fibrils more attenuated elongated fusiform bodies are found, the extremities of which present long and fine points. These bodies can be easily isolated, although their fine extremities adhere intimately to the fibrils. With a proper degree of care we may convince ourselves of their essential independency, and may follow many of the fibrils from one end of the tendon to the other, as smooth homogeneous threads without any indication of nodal points. This, as has been above stated, is only possible whilst the cells are still proportionately broad and short. The further process of development consists in the great increase in the number of the fibrils, in the separation of the cells from one another, and in their becoming gradually more and more completely atrophied. In recently born children, and in adults alike, the atrophied fusiform cells, as appears from what has already been stated, present the same aspect as at all periods of embryonic life, and we never in any instance find a cell intercalated in the course of a fibril.

From these observations it follows that, in the foregoing cases, any development of the fibrils by the growth of cell processes must be regarded as questionable.

The fibrils appear to be formed simultaneously for considerable portions of their length. The cells contained in the embryonic mass which is destined to form connective tissue, either all increase in the process of development to fusiform cells of considerable length, at the same time separating from one another in such a mode that at first a small, but subsequently gradually increasing number of fibrils appear between them, as in the tendons, or that at first a transparent, interruptedly striated substance occurs in great quantity, in which the fibrils become apparent at a later period, as in the peritoneum. This is what, in brief, I believe every one may convince himself of.

As regards the significance of the large quantity of homogeneous substance which undergoes fibrillation in the peritoneum, with coincident elongation of the cells, it is difficult to make any positive statement. It can only be said, with certainty, that the fibrils originate at the expense of a large continuous mass by a kind of transmutation.*

Further investigation has shown the original interpretation of Schwann to be the correct one, and that the fibrillæ of connective tissue take their origin from elongated cells, either by the splitting up of the cell body into fine fibrillæ, or by the body of the cell becoming drawn out into one long fibrilla.†

The most probable view then is, that the homogeneous intermediate substance which appears at a certain stage of development in the peritoneal lamina originates in a continuous metamorphosis, extending irregularly towards the central portion of the rapidly enlarged cell substance of the formative cells. The lamina thus originating in the fusion of the metamorphosed cell substance becomes secondarily perforated with smooth-edged foramina, whilst a continuous conversion into fibrils takes place.

As regards the growth of connective and tendinous tissue, the breadth of

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* I extract from a letter of Babuchin to Stricker that Babuchin has convinced himself of the development of cells into fibrils in the gelatinous tissue of Fishes. He admits, however, that what he terms Fibrils, under certain circumstances contracted themselves towards the nucleus of the cells which became round, and then commenced anew to send forth processes. This latter statement furnishes me with the strongest evidence that Babuchin in his preparations has not had to deal with the fibrils of connective tissue.

† Breslauer, Max Schultze's *Archiv*, Band v., 1869.

the fibrils in the fœtus amounts, according to Harting,* to 0·0010—0·0014 millimetres, and in the adult to 0·0007—0·0017 millimetres. As the fibres, therefore, do not increase in thickness, their numbers must augment. The amorphous connective tissue between the fasciculi of the tendons becomes larger in quantity. The tendinous fasciculi increase, not only in number, but in thickness. In reference to the latter fact, Obersteiner† has shown that the points from which the new formation proceeds are partly situated between the old fasciculi and the investing connective tissue, and partly in the investing connective tissue itself.

Observations have been made by Sertoli,‡ showing that the development of the reticulum and of the adenoid substance of the lymphatic glands proceeds from embryonic connective tissue, composed of a mass of uniform cells.

As regards the Ligamentum pectinatum iridis, the trabecular tissue in embryos of five months old may be distinctly seen to consist of branched flattened cells, the substance of which is homogeneous and condensed, whilst in these trabeculæ remains are still visible of nuclei that at a later period become atrophied.

In regard to the genesis of the elastic fibres, very various views have at different times been expressed. Their origin from nuclei, which Henle long ago believed he had perceived, has been by Henle§ himself rendered doubtful. It has also been proved that they do not develop from cells in the mode described by Donders.‖ The opinion is now generally held that there is an actual deposit in the form of fibres.¶

It is remarkable that the fibres, after their deposition, increase in thickness.

Fat Cells in Connective Tissue.—In various parts of the animal body the connective tissue contains great numbers of cells, which, enlarging equally in all their dimensions, attain a considerable size, and have in their interior a large fat drop, completely filling them. The diameter of these cells reaches, in man, 0·2 millimetres. Their form is round or somewhat oval. Where such fat cells are deposited in great number in the connective tissue, they are divided into separate groups, or lobules, by strong trabeculæ. Each of these lobules possesses its own system of vessels, which, with their branches, reach into the interior from the surface, and are accompanied with fine bundles of connective tissue; here they divide into such numerous capillaries, that the smaller groups of cells, or even the individual fat cells, are surrounded by vascular loops.

Certain regions of the body in man are especially characterized by the presence of such adipose tissue. Thus it occurs in the subcutaneous connective tissue, or panniculus adiposus, which is very abundant in various parts of the body, as in the mammary gland of the female, the pubic region, buttocks, and sole of the foot; in other parts it is less developed, but is only absent in some few places, as the eyelids and male sexual organs. Adipose tissue, moreover, is found in the omentum, mesentery, beneath the pericardium of the heart, and on the great vessels, around the kidneys, in the orbit, and in the fat humps and adipose masses formed in the bodies of certain animals, etc.

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* *Recherches Micrométriques sur le développement des Tissus*, etc., 1845, p. 53.
† *Loc. cit.*
‡ *Wiener Akademie, Sitzungsberichte*, Band liv., p. 149.
§ Canstatt's *Jahresbericht für* 1851, p. 22, Band i.
‖ *Zeitschrift für wissenschaftliche Zoologie*, Band iii.
¶ Henle, *loc. cit.* Reichert, Müller's *Archiv*, 1852, p. 94. H. Müller, *Würzburger Verhandlungen*, Band x., p. 132; *Bau der Molen*, 1847, p. lxii.

In the fattening of animals, or in commencing obesity in man, the adipose tissue increases at these points, and occurs in large quantities also in regions of the body that with less abundant supplies of food remain free from fat; as, for example, in the connective tissue between the muscles.

In large and fully developed fat cells, a thin smooth membrane can be distinguished surrounding the oil drop, which, however, collapses and becomes folded, if the cells are burst by pressure, and the contained drop of oil be allowed to escape. The membrane of the fat cells can also be brought into view in a crumpled state by boiling the tissue with strong alcohol and ether.

The oil drop contained in these cells presents a faint yellow tint in man, but in various animals many other tints occur. In the fresh cells, both of cold and warm-blooded animals, the fat is fluid. On cooling, it solidifies with great facility, especially in the latter class of animals. This last process occasions a flattening of the closely compressed cells, and their oily contents may frequently be observed to crystallize partially in needles which are collected in the form of a brush. When this occurs, a single spicule or a crystalline stella, composed of many spicules, appears on the surface of the fat cells.*

Besides the large fat cells enclosed in a smooth membrane, which are most abundant in fully developed adipose tissue, other cells also occur which are smaller, and in which the oil drops are invested by a layer of granular cell substance; this, when seen in profile, appears in the form of a rather broad ring around the oil drop. Cells presenting this aspect are frequently found at the borders of fat lobules, as in newly formed adipose tissue, whether in the embryo or in the adult. The formation of the adipose tissue may be excellently followed in the omentum of animals as well as in certain cases of sudden death in man. In the first stage of their development, the cells that subsequently form fat cells appear as small round granular bodies, provided with round nuclei, and presenting all the characters of young cells. In the interior of these a few small strongly refractive oil drops first originate, which, however, usually soon collect to form a single large fat drop, occupying the middle of the cell. Much less frequently several large drops are found close to one another.

The protoplasm of the cells in which such large drops have developed, lies like a cincture around the drops, presenting everywhere nearly the same breadth, except only where the nucleus is imbedded in it and forms a thickening or projection that causes the whole protoplasmic mass to be comparable to a signet ring.

During the succeeding stages of development the cells undergo continuous increase in size, the oil drops in particular becoming larger. The investing protoplasmic layer, whilst it progressively diminishes, though not proportionately to the enlargement of the fat drops, preserves its original granular appearance. The nucleus is always visible, but, concomitantly with the increase of the oil drop, and the expansion of the surface of the protoplasmic layer, is constantly pressed outwards. In the final stages of development the remains of the original investment of protoplasm consist only of a thin homogeneous membrane, on some part of which the nucleus, now become somewhat more homogeneous and diminished in size, may always be demonstrated. The nucleus is best seen in cells treated with Müller's fluid, and then stained with carmine.

If we institute a comparison between the fat cells in various stages of

* Henle, *Allgemeine Anatomie*, p. 393.

their development, it becomes immediately apparent that the protoplasm originally present does not merely expand coincidently with the enlargement of the cells, but that as the cell attains its full growth, and becomes invested with the above-mentioned membrane, the protoplasm also augments in quantity.

We possess no information from direct observation, of the relation in which the protoplasm of the cell and the contained oil stand to one another in regard to their nutrition.

It is, however, certain, that whenever a new formation of adipose tissue occurs, a supply of histogenetic substance in the form of young cells first occurs, which is followed by a supply of material for the growth of these cells.

In consequence of hunger and disease, the fat cells lose their oil and become filled with a serous fluid. In rabbits, Czajewicz* has observed the fat to disappear during abstinence from food in the course of a few days, and with equal rapidity, when abundant nutriment was supplied, reappear in the original cells.

Cartilage.

Of this tissue those organs of the animal body are formed either wholly or partially, which have long been noted in anatomy on account of the persistence of their morphological characters and great pliability, or from their peculiar consistence when cut. In histology, the distinction formerly made into proper (true, hyaline) cartilage, and fibrous cartilage is no longer admissible, since it has been shown that just as the former consists of cells imbedded in a transparent and apparently uniform matrix, the latter is composed of similar cells in a matrix traversed by fibres.

True or Hyaline Cartilage contains cells provided with nuclei (cartilage corpuscles) lying in cavities of various size and form distributed through an amorphous matrix, and the corpuscles closely resemble the cavities in their form.

In order to demonstrate these points, it is only requisite to make very fine sections of fresh cartilage. If it be desired to investigate cartilage in a physiologically fresh condition, only indifferent fluids can be employed, as in the case of connective tissue. For such observations those cartilaginous plates of cold-blooded animals which can be easily isolated from the soft parts, and are as thin as ordinary sections—as, for example, the ensiform process or the episternal cartilage of the frog, or the thin cartilaginous plates of the shoulder girdle of tritons—are preferable.

In such cartilages, the cells lying in the interior of the cavities appear when fresh as transparent, finely granular masses completely filling them up, and resembling the protoplasm of other cells. A small number of large granules are found in their interior, together with a well-defined round nucleus, containing several strongly refractile, large, and bright molecules, which are usually larger than those found in the protoplasm of ordinary cells, causing the nucleus, when compared with these, to present a coarsely granular appearance (fig. 17); the nucleus occasionally appears transparent and vesicular, with double contour lines and a single nucleolus. Two nuclei may frequently be seen in one cell. If, as in the case of connective tissue, an indifferent fluid be applied, like the aqueous humor, or serum diluted with distilled water, a cloudiness first occurs in the granular cell substance;

* Reichert and Du Bois' *Archiv*, 1866, p. 289.

the fine molecules originally present become partially concealed in portions of the cell substance which have rolled themselves into ball-like masses, and soon a shrivelling of the cell becomes apparent, so that it either partially or entirely separates from the wall of the cavity in the cartilage; as a consequence of this a transparent ring appears between the inner surface of the cavity and the shrivelled cell, or the cell may still remain attached to certain points of the wall of the cavity, and is then irregularly stellate; such long and more firmly adhering processes of the already partially shrivelled cell usually detach themselves sooner or later, but do not shrink in the same proportion, so that even when completly detached from the walls of the cavity such cells appear to be irregularly beset with processes. If these appearances, which long remain unaltered, have been produced by the action

Fig. 17.

Fig. 17. Fresh cartilage from the Triton.

of water, it may be seen that in some cells the nucleus has become indistinct, its place being indicated only by a dull spot; whilst in others it still appears distinctly defined. By changing the focus some of the indistinct nuclei may be more clearly brought into view, but others always remain indistinct; and these differences appear to depend upon the varying position of the nucleus in the cell, in consequence of which the greater part of the latter is sometimes above and sometimes below the nucleus in relation to the observer. Similar changes to those induced by the addition of water occur in the cartilage cell on the addition of saccharine and saline solutions. Dilute solutions of potash and soda, and also of acetic acid, produce very similar effects.

The experiments of Heidenhain* have shown that powerful induction shocks cause contraction of the cartilage cells, render them irregular in shape, and detach them altogether or in part from the wall of the cavity. This was first observed by Heidenhain in the cells of the cartilage of the head of tadpoles, and in the articular cartilages of the adult frog. In the former he also saw the molecular movement of granules previously visible in the cells effectually stopped. In shrivelled cells there further occurred an

* *Studien des Physiologischen Instituts zu Breslau*, Heft 2. Leipzig, 1863, p. 1.

accumulation of clear drops, or similar drops were thrust out into the cavities of the cartilage. The first action of the induction current is to produce a cloudiness in the interior of the cells, which often suddenly traverses them like a shadow. Heidenhain regards these phenomena as the expression of commencing coagulation, as are also all the changes induced by induction shocks, since he was unable to observe that the death of the cells was accompanied by any return to their original condition.

If one of the above-described induction apparatuses be used in order to apply a few opening shocks to the ensiform cartilage of the Frog (Rana temporaria), covered with a covering glass, and placed without addition of fluid upon tin-foil electrodes closely connected with one another, it will be found that an entire series of such shocks are always required to produce a distinctly visible change in the cells, or a long period after the application of a shock must elapse in order to allow the very slowly following change to become apparent. The cells of the cartilage of Tritons behave themselves very differently in this experiment. Here a single shock is sufficient to cause the cells to contract rapidly, and even quite suddenly, under the eyes of the observer, like transversely striated muscle when irritated; indeed, even the iron core may be removed from the primary coil, and the seconda-

Fig. 18.

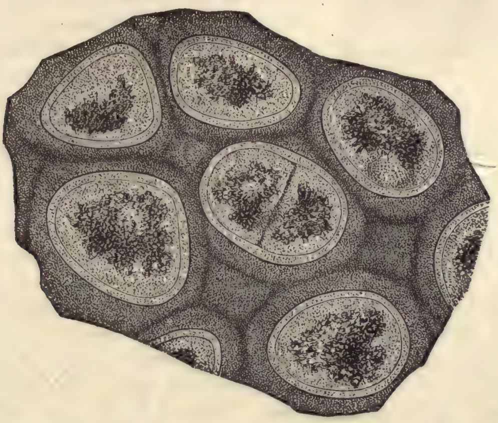

Fig. 18. Cartilage from a Triton after a single opening shock of induced electricity.

ry coil of the apparatus previously quite thrust home may be withdrawn to considerable extent, and yet the strength of current will still be sufficient to produce the same results with a single shock. The cells which have thus been made suddenly to undergo contraction (fig. 18) appear coarsely granulated, darker than before, with the nucleus scarcely, if at all, perceptible; whilst alteration of the focus, and close inspection of the edges of the cells after they have been separated from the cavity, shows that the immediate cause of their altered appearance is that their surfaces have become mulberry-like (fig. 18). In this condition the cells may remain and be examined for hours, or even for days together, if they are preserved from the effects of evaporation by the employment of the moist chamber. A slight enlargement, accompanied by increased smoothness of the surface, may frequently be observed; the nucleus at the same time becoming somewhat more dis-

tinct; but the cells always remain more opaque than before the passage of the current, and never completely recover their original appearance. Nor are any satisfactory results obtained if the attempt be made to restore the cartilage to its normal condition by introducing it again beneath the skin of the animal. The cells do not recover their previous appearance even four and twenty hours or more after the application of the electric shock. For the second observation some portions of the cartilage should be preserved which were not situated between the electrodes in the first experiment for the sake of comparison. It must be admited that a vital contraction of the cartilage cells has not been clearly proved to occur so long as it has not been shown that they are not liable to alterations of quiescence and activity, or, in other words, do not undergo amœboid changes of form. The effect which a single induction shock produces in the cartilage cells of Tritons renders it, however, highly probable that their diminution is due to a contractile power. On a warmed stage an alteration in the cartilage cells of Frogs and Tritons is first observed when the temperature rises to 73° or 75° C. (163°—167° Fahr.); the cells then become cloudy, in consequence of the formation of a granular coagulum. Nothing further has been remarked respecting the differences in the peculiarities of the cells of hyaline cartilage in various animals besides that which we have above stated in regard to the cells of the Frog and Triton. The observations made by Reitz* on the cells of the tracheal cartilages excised from Rabbits, in reference to the formation of cicatrices, and their behavior in inflammation of the trachea produced by caustic ammonia, are well worthy of notice. In these experiments the cartilage cells in the cicatricial tissue were seen to assume the form of elongated fibres, and those of the irritated cartilage to become mulberry-like, with numerous deep depressions, as though about to divide. That wounds of cartilage heal by connective tissue is an old observation.†

As a general rule the appearance of the cells of hyaline cartilage agree more closely with the formerly described characters of fresh cartilage from the Amphibia, the more recent they are when brought under examination.

In cartilages longer removed from the body the cell substance appears cloudy and shrivelled, and more or less completely detached from the wall of the cavity; the nucleus varies in distinctness, and is sometimes homogeneous and sometimes granular. Cells are frequently observed in the costal or laryngeal cartilages, containing deep yellow-colored drops (of oil), surrounded by dark rings, more or less strongly refracting light. Similar drops are often found free in the cavity of cartilage, external to the shrivelled remains of the cell.

The cells, and the cavities of the cartilage in which they are lodged, are separated by a variable amount of the matrix; they, moreover, sometimes lie detached and separate at regular distances, whilst at others they are united together into groups of few or many cells; and these again may be separated from one another by wide intervening spaces or by a few solitary cells. Two or more cells lying in close proximity to one another are frequently seen to occupy the same cavity. The form of the cartilage cavities is spheroidal, ellipsoidal, or elongated and fusiform, or somewhat flattened and lenticular; the two latter forms occurring closely compressed together, near the free surfaces that play over one another in joints, or in many of

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* *Sitzungsberichte der Wiener Akademie*, Band lv., p. 501.

† See G. H. Weber on this subject in Hildebrandt's *Anatomie*, Band i., p. 305. More recently, Redfern has published his observations on the same subject. See Henle, *Jahresbericht für* 1851, p. 52; also Klopsch, *Zeitschrift für klinische Medicin*, 1855.

those cartilages whose surfaces are invested by perichondrium, and the cells then lie with their long diameter parallel to the surface; whilst in the more centrally situated portions of these cartilages are the larger cavities of the first-named varieties, and between these and the most external, various transitional forms. At points where cartilage and bone tissue are in immediate apposition the cartilage cells are frequently found to be arranged with great regularity in longitudinal rows in the direction from the bones towards the free surface of the extremity invested with cartilage. The cells in these longitudinal rows will be subsequently considered in treating of the subject of ossification. The cartilage cavities occasionally present a stellate form. Statements to this effct may be found in the writings of Leydig,* where he is describing the skull of the Chimæra and various Plagiostomatous fishes. Stellate cells have also been found by Kölliker† (in softer parts?) in the tracheal cartilages of oxen.

The matrix of hyaline cartilage, when in a perfectly fresh condition, and examined in thin sections or laminæ with very high powers, often presents a thoroughly homogeneous appearance. But it also happens that in recent and very transparent cartilages, especially in those in which the cells lie close together—as, for instance, in the earlier-mentioned examples of cartilage from the Frog and Triton—the cells are apparently surrounded by clear rings of equal breadth; and that the small trabeculæ extending between the adjoing cells only represent the circular layers investing these cells. In the older cartilages of various animals and of man there may also frequently, but not always, be seen a similar circular area which sometimes appears as though composed of several concentric rings. According to Max Schultze, this appearance is very beautifully exhibited in the cartilage of the Myxine. These rings represent the transverse section of the successive shells deposited around the cartilage cells, constituting the so-called membrane of the cartilage cell, or cartilage capsules of authors. We shall learn their significance hereafter. By the application of certain reagents, as, for instance, diluted sulphuric acid and chromic acid,‡ or a mixture of water, nitric acid, and chlorate of potash, or by digestion in water, at a temperature of from 35° to 40° C.§ (95° to 104° F.) (in which case the addition of acids, in order to convert the connective tissue as usual at a lower temperature into gelatine, operates very effectually) the matrix of the cartilage, hower homogeneous it may appear to be in the fresh condition, may be split up so completely into a number of layers arranged concentrically around the cells, that nothing remains besides them; and, indeed, in more fully developed cartilages a series of precisely similar shells succeed that which immediately surrounds the cell; or there may appear two or more closely approximated cells, with their primary capsules enclosed in secondary capsules, and groups of the latter again enclosed in still larger ones. It is only in cartilages with sparingly distributed cells that a portion of the firm matrix at a great distance from the cells surrounded with concentric areas, remains unlaminated after the operation of the above-mentioned agents.

The imbibition of the red coloring matter of anilin is well adapted to exhibit the layers of the capsule.‖ The lamination of the tissue is also excellently shown by the action of chloride of gold, and very beautiful preparations can be obtained by protracted treatment with this agent, in

* Müller's *Archiv*, 1851, p. 241.
† *Gewebelehre*, 1867, p. 69.
‡ Fürstenburg, Müller's *Archiv*, 1857, p. 1.
§ Heidenhain, *loc. cit.*, pp. 23 and 25.
‖ Landois, *Zeitschrift für wissenschaftliche Zoologie*, Band xvi., p. 11.

consequence of the deep color communicated by the reduction of the metal.

If diluted sulphuric acid or concentrated hydrochloric acid acts for a long time upon these sections of cartilage, the largest capsules first dissolve, and then the secondary ones. Those which immediately surround the cells are the most resistant. Moreover, if sections of cartilage are long boiled, we may first remark the above described lamination of the matrix, and then successive solution of the capsules in the order above given. All the operations consequently lead to the isolation of the cells still invested by their capsules, providing they are subjected to their influence only for a certain definite period. The observations above adduced completely negative the views of those who regard the clear rings around the cartilage cavities as a mere optical phenomenon, and who deny the existence of the cartilage capsule.*

The ultimate result of continued boiling is, however, that the coagulated cells alone remain.† The solution obtained from cartilage after exposure to a boiling temperature for twenty-four hours, or for a few hours only at a temperature of 120° C. (248° F.), gelatinizes on cooling like gelatine itself. It does not, however, contain gelatine, but the material distinguished from gelatine by Johann Müller, by the name of Chondrin. The opposite statement of Friedleben ‡ has been disproved by Wilkens§ and Trommer.‖ The chondrin-giving substance of cartilage, unlike the gelatine-yielding substance of connective tissue, does not swell up in water. Acetic acid causes it, when obtained from some cartilages, to become somewhat clearer, whilst in others it renders it cloudy. It does not cause it to swell up.

After exposure for from eight to twelve hours to the action of solution of osmic acid, containing one-fortieth per cent., thin sections of cartilage exhibit a system of dark striæ, usually running in a straight direction through the matrix, which frequently connect the several cell cavities with one another. Bubnoff,¶ in describing these striæ for the first time, expresses his opinion that they are to be regarded as juice canals.

The divisibility of the matrix of hyaline cartilage into capsules of various orders, or cell territories as they have been termed, shows that we cannot regard the matrix as an excretion of an amorphous and uniformly dense intercellular substance between the cells, as was formerly held to be the case before the exact value of the facts above stated was recognized; though this is a view to which we shall again refer in our account of the development of hyaline cartilage. It has not yet been shown whether, in hyaline cartilage, an intervening material different from the chondrin-yielding substance, and which, if present, would be in smaller quantity than the former, really exists or not.

The various parts of the embryonic skeleton are formed from hyaline cartilage, whilst in adults it constitutes the cartilages covering the articular ends of bone, and the opposed surfaces of the symphyses, the ensiform process, the ribs, and lastly, the bronchial, tracheal, and laryngeal cartilages, with the exception of the epiglottis. In the lower Vertebrata, Fishes, and

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* Bergmann, *Disquisitiones Microscopicæ de Cartilagine. Mitau und Dorpat*, 1848.

† Hoppe, *Archiv für Pathologische Anatomie*, Band v., p. 174. See also Mulder and Donders in G. J. Mulder's "Essay on General Physiological Chemistry;" Donders, in *Holländische Beiträge, Düsseldorf u. Utrecht*, 1846; Zellinsky, *De telis quibusdam collam edentibus, Diss. inaug.* Dorpat, 1852.

‡ *Zeitschrift für wissenschaftliche Zoologie*, Band x., p. 20.

§ *Idem*, p. 467.

‖ Virchow's *Archiv*, Band xix., p. 554.

¶ *Wiener Sitzungsberichte*, 1868, April.

Amphibia, considerable portions of the skeleton, which are ossified in other animals, remain cartilaginous throughout life; whilst in some animals cartilages occur in parts which, in others, and in man, consist only of connective tissue; as, for instance, the sclerotic coat in the eye of Birds, Amphibia, and Fishes. In regard to the Invertebrata, descriptions have been given of the distribution and occurrence of cartilaginous tissue, in the case of Cephalopods and Molluscs, by Lebert and Robin,* and by Claparéde and Semper.† Before we pass to the consideration of fibro-cartilage, the fibrous transformation of the matrix of hyaline cartilage must first be mentioned, which occurs sooner or later after the commencement of extra-uterine life. This appearance is particularly obvious in the costal and laryngeal cartilages.‡ On examining a transverse section of the costal cartilages of an adult, striæ or rings may almost always be observed, distinguished by their white and opaque appearance, and the peculiar lustre they possess. Microscopic examination shows that the matrix at these points is composed of rigid closely approximated parallel fibres. These are unbranched, and when subjected to the action of acetic acid, do not disappear, but pass uninterruptedly into the surrounding non-fibrous portion of the matrix. If such a section be broken up with needles, the parallel fibres break at various points of their course, and these project to a variable extent from the fractured

Fig. 19.

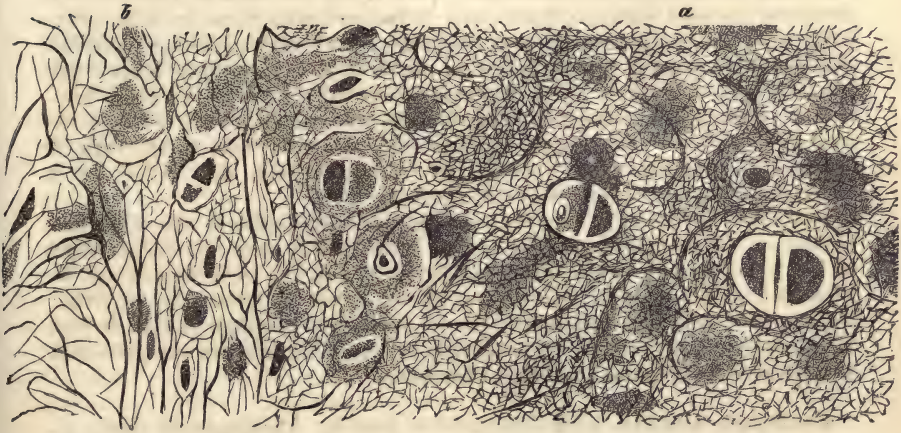

Fig. 19. Section of the boiled and dried auricle of the ear of Man; *a*, retiform cartilage; *b*, connective tissue.

surface; the cause of this development of fibres in hyaline cartilage is not accurately known. Coincidently with the formation of these fibres in cartilage, a process of proliferation usually occurs, so that the cells lie closely compressed in great masses in the matrix.§

* Müller's *Archiv*, 1846, p. 129.
† *Zeitschrift für wissenschaftliche Zoologie*, Band ix., p. 274.
‡ Donders, *Holländische Beiträge*, Band i., p. 258. H. Meyer, Müller's *Archiv*, 1846, p. 292.
§ Donders, Meyer, *loc. cit.*

FIBRO-CARTILAGE.—True fibro-cartilage differs from hyaline cartilage in its matrix, presenting fibres of variable number, form, and chemical characters. The alteration of the index of refraction occasioned by the layers of delicate fibres and their interstices, and in some fibro-cartilages the small degree of translucency possessed by the several fibres, makes even fine sections of these cartilages, when compared with hyaline cartilage, appear on examination much darker and more opaque. By direct light, on the other hand, the fibro-cartilage appears whiter or more yellow in comparison with the hyaline variety. It is less brittle, but often cleavable in certain directions. The latter circumstance enables a mechanical isolation of the cells, on breaking up such sections of cartilage, to be much more easily accomplished than in hyaline cartilage.

The fibres of *elastic or reticular cartilage* (fig. 19) appear dark, of unequal thickness, branched, and often intercommunicate by very numerous anastomoses, thus forming a very fine but often wide-meshed plexus. In their general characters and capability of resisting the action of acetic acid and alkalies, they agree with elastic fibres. In many instances, as in the cartilage of the ear of man, and the epiglottis, it may be shown that these fibres are uninterruptedly continuous with the elastic plexus of the connective tissue investing the cartilage (Donders). The close fibrous plexus often reaches to the margin of the cavities, which contain the cells of the cartilage, but frequently a homogeneous capsule remains around the cartilage in the form of a clear ring, whilst a considerable quantity of the matrix between the fibres may remain distinguishable, and both conditions occur in close proximity with one another in the same cartilage. As various cartilages present differences in respect to this point, so do we find some giving more some less chondrin on boiling. The fibrous material does not itself undergo solution on boiling. A beautiful object for the observation of the above-mentioned transition of the elastic fibres of cartilage into those of the skin, is afforded by sections made through the auricle of man, first boiled for a short time as a whole, and then dried (see fig. 19).

Moreover the fibres of the fibro-cartilaginous extremity of the processus vocales of the arytenoid cartilages pass immediately into the elastic fibres of the vocal cords.* This latter fact is opposed to the view maintained by Gerlach,† of the specific distinctness of the fibres of plexiform cartilage. The parts composed of elastic fibrous—or retiform—cartilage consist in man of the auricle of the ear, of the epiglottis, and the extremity of the processus vocales of the arytenoid cartilages (Rheiner).

CARTILAGE MINGLED WITH CONNECTIVE TISSUE.—Cartilaginous tissue occurs, and frequently in very considerable masses, imbedded in connective tissue. Efforts have in consequence been made to establish a special group of fibro-cartilages, the connective-tissue cartilages; but it would appear to be more correct to describe these structures as mixtures of the two tissues. Such mixtures occur in the interarticular cartilages, the glenoid cartilages, the cartilages of the symphyses, at the articular extremities of the clavicle, and the corresponding articular surfaces of the scapula and sternum (Henle), and in the tarsal cartilages of the eyelids. With these must also be enumerated the tendons and tendinous sheaths containing cartilage. Such tendon-cartilage may be frequently observed in the tendons near their attachments to bone. The Tendo Achillis of the Frog must especially be

* Rheiner, *Beiträge zur Histologie des Kehlkopfes.* Würzburg, 1852.
† *Gewebelehre*, p. 124.

mentioned as presenting large cells with round nuclei, which may be regarded as cartilage cells, and which are present in considerable numbers.*

Also the appearance which has already been described in the digital tendons of the Frog may again be alluded to. The same features are presented by other tendons, especially amongst the Amphibia. It must, however, here be stated that objections have been raised to considering these cells to be cartilage cells.† It is certain that in the cells of these tendons of the Frog no chondrin-yielding substance can be proved to be present. In preparations treated with chloride of gold, masses of equably stained protoplasm are found in close apposition.

Parenchymatous Cartilage (Cellular cartilage).—We must now describe a form of cartilage which possesses no matrix, the so-called parenchymatous cartilage. Kölliker ‡ has also sought to introduce this type amongst the tissues. Thus, amongst the cartilages without intermediate substance, he enumerates the chorda dorsalis of embryos and of many adult fishes, numerous fœtal cartilages, some parts of the cartilage of Myxinoid fishes, a part of the branchial laminæ of fishes, the cartilage of the Tendo Achillis of the Frog, and of the outer ear of many Mammals; the cartilage entering into the structure of the Geryonia, Annelida, Cephalophora, and of Limulus. This grouping, however, is decidedly imperfect. Kölliker distinguishes between the capsule or membrane of the cartilage cells, consisting of chondrin-yielding substance, and an intercellular substance existing between the cells, but also yielding chondrin on boiling; but, inasmuch as all the chondrin-yielding substance of cartilage is referrible to the capsules, a number of the cartilages described by Kölliker as destitute of intermediate substance must be regarded as belonging to the hyaline cartilages. How far, on the other hand, we are justified in speaking of naked cartilage cells, and of considering the cellular form of cartilage as composed of them, is not as yet determined.

On this point we can only refer to embryological observations, and to others based on comparative anatomy, and thus allude, for instance, to the early stages of cartilage, to the primordial cells of cartilage and the tissues composed of them.

In order, however, to diagnose the cells as cartilage cells, of whose history and development we have no information, it is requisite that we should be better acquainted with their internal organization than at present, as well as with the differences that exist between cartilage cells and other masses of protoplasm. Other difficulties similar to those that are here met with in regard to the limitation of the cartilaginous tissue, frequently arise when the identification of cells is under consideration. Experiments undertaken to determine whether in the cells contained in the Tendo Achillis, and in the digital tendons of the Frog or Triton, similar phenomena follow the application of induction shocks to those observed in the cells of the hyaline cartilages of these animals, have altogether failed.

Development of Cartilage.—Hyaline cartilage exhibits in most instances an unmistakable similarity to the first rudiments of all animal tissues, in being composed of cells advanced to a nearly equal grade of development.

* Kölliker, Lehmann, *Zeitschrift für wissenschaftliche Zoologie*, Band xiv., p. 109, Taf. 14.

† Gegenbauer, *Jenaische Zeitschrift für Medicin und Naturwissenschaften*, 1866, p. 307.

‡ *Gewebelehre.* Leipzig, 1867, pp. 66, 67.

The investigations of Rathke* on chickens, and of Kölliker † on tadpoles, have taught us that the embryonic cells whilst still filled with yolk granules, as they gradually increase, become more transparent; and then becoming separated from each other in consequence of the development of rods of a homogeneous and transparent substance, finally constitute the first rudiments of embryonic cartilage.

As soon as the matrix has become distinctly differentiated from the previously closely compressed cells, it forms a homogeneous clear ring around each, and between these rings run fine lines resembling the contour lines of epithelial cells. At this period, therefore, the cartilage consists of cells which are contained in polyhedric capsules, and no special artifice is required in order to isolate the cells completely, together with their capsules. The costal cartilages of young sheep, or of human embryos kept in Müller's solution, can easily at this stage be split with needles into laminæ.

In pursuing the further development of cartilage, the question arises of the capacity of cartilage cells to undergo division. Cells in the act of division, or apparently originating from the division of cells, are frequently met with, not only in embryonic cartilages, but also in those of adults. Thus, in the first place, cells may be observed containing two nuclei. It has also been stated that the nucleoli are sometimes double, nor is it difficult to demonstrate this in the cartilages of tadpoles. The division of the nucleus has even been directly observed (as recently by Kölliker).‡ The occurrence of two nuclei appears, however, to be the only condition which is of frequent occurrence and easily observed. § It it not easy to decide whether in these cases two new nuclei have originated in the place of one nucleus that has undergone absorption, or whether the division of the nucleus on account of its rapidity has escaped observation. The division of the cell itself may, indeed, be readily followed, since it depends on the formation of a groove encircling the cell. It cannot, however, be stated that the division leads in the first place to the formation of two nucleated protoplasmic masses, lying in a common capsule. It would rather appear that the division of the protoplasm is very intimately associated with the formation of a capsular investing sheath for the daughter cell. However closely the cells under observation lie in apposition to one another, it is still observable when they are detached from the walls of the cavity by some of the above-mentioned means that the cavity is itself divided by a thin septum into two chambers. The differentiation of parts in the entire plane of division consequently takes place with great rapidity. The daughter cells are capable of forming complete capsules, which gradually increase in thickness, and are clearly to be distinguished from one another, not only where they are in contact, but also where they touch the capsule of the mother cell.

The daughter cells orginating in division can in like manner produce a new generation, leading to enlargement of the spaces enclosed by the capsules of the mother cells.

The cells then appear to be arranged in detached groups at a considerable distance from one another, and the youngest capsules are now more distinctly visible. After the application of the means which have been above described, the whole matrix again presents the appearance of being divisible into nests of capsules, one enveloping the other.

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* Froriep and Schleiden's *Notizen*, Band ii., 1847, p. 305.

† *Mikroskopische Anatomie*, Band ii., p. 349.

‡ *Gewebelehre*, 1867, p. 24.

§ Frey, *Histologie und Histochemie.* Heidenhain, *loc. cit.*

If we further compare the appearances presented by embryonic cartilage with the fully developed cartilage of adults, we must admit that the cells, without undergoing division, are capable of producing successive generations of capsules, fresh ones constantly forming in the interior of the old, whilst the external ones increase in size, and become faintly marked as regards their limits. In such cartilage the cells appear fewer in number, and the matrix of the cartilage just formed can be frequently artificially split into concentric rings surrounding the cells. In fully developed cartilage, moreover, both laminated mother and daughter cells may be coincidently observed.

Observation of the development of cartilage thus teaches us that in its earliest stages cells destitute of cell membrane or primordial cells are alone present, and that the so-called matrix or chondrin-yielding substance of cartilage is a secondary formation. Opinions are, however, divided respecting the relation which the latter bears to the former.

On the one hand the chondrin-yielding substance may be regarded as a purely intercellular material, which is either deposited between the cells from without, or is a secretion of the cells themselves. In order to explain the nature of the capsules (including the youngest) it must be admitted on this view that the intercellular substance in the vicinity of the cells is differentiated by a peculiar (?) process of condensation from the remaining intercellular substance.*

In complete opposition to this exposition of the nature of the matrix is the view propounded by Remak,† to the effect that the young cartilage cells are provided with two membranes, of which the innermost corresponds to the primordial utricle of the vegetable cell. In the act of cell division this last alone participates. The proper substance of the cartilage is deposited either between the external and internal membranes, or between the former and the daughter cells, and indeed, in the first instance, on the inner surface of the external membrane; and in this mode the vesicular cavities in the cartilage arise. Each newly developed daughter cell immediately forms again an external membrane, upon the inner surface of which fresh cartilage is deposited, whilst the cells again subdivide; and there is thus developed a nest of cartilage cells contained one within another. By the fusion of the several cartilaginous laminæ with one another, and the disappearance of the cell membranes which served as a framework for its deposit, the matrix of the cartilage is produced, which thus appears to be an intercellular formation, and may be called "parietal substance." It is easy to perceive that the views of Remak were constructed on the cell theory of his day.

If, however, we abstract the two hypothetically present membranes of Remak, the formation of chondrin-yielding substance, described by him, and its relation to the cells, corresponds exactly to the processes observed in the development of cartilage, and to the appearances which may be obtained by breaking up mature cartilage. Fürstenberg, who was the first to accomplish this, regarded the layers of chondrin-yielding substance as thickened cell membrane, and showed that in certain cartilages the whole matrix was to be considered as composed of such thickened membranes belonging to successive generations of mother and daughter cells. Kölliker‡ also maintains the capsules of cartilage to be cell membranes, and to represent the secondary membrane of the vegetable cell. In some few cartilages the matrix is composed of these alone, but in others again, especially in those in which the di-

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* Aeby, *Zeitschrift für rationelle Medicin*, Band iv., 3 R., p. 43.
† Müller's *Archiv*, 1852, p. 69.
‡ *Gewebelehre*, 1867, p. 64.

vision into cell territories is not completely effected, a large and often the chief part of the matrix is formed of pure intercellular substance lying between the cell membranes. Kölliker's view is unsatisfactory on account of its attributing a double and consequently fundamentally distinct mode of origin to one and the same substance—that, namely, which yields the chondrin; and it is unlikely, therefore, to be correct. If, however, we adopt the view of Fürstenberg, which may be directly proved in the case of many cartilages, it is easy to show that in those cases where the lamination of the matrix is not completely accomplished, a portion of the original cell boundaries vanishes after the action of reagents, just as in most cartilages before the action of reagents they are likewise indistinguishable. It still, however, remains a question whether we shall represent the generations of capsules, of which the matrix of cartilage is composed, as new formations proceeding from the surface of mother and daughter cells, or as metamorphosed superficial layers of the cell protoplasm. The latter view is held by Max Schultze, Brücke, and Heidenhain; the two latter investigators, however, remark upon the difficulty of disproving the opposite view, and Heidenhain refers to cases where minute cells are surrounded by strong laminated capsules. It remains to be investigated whether isolated cells can undergo complete chondrogenous metamorphosis, and whether it can thus be explained how it happens that the matrix is frequently to be observed destitute of cells for a considerable extent.

According to Harting's researches on the cartilages of the ribs, the cartilage cavities increase in size throughout the period of fœtal life and also after birth. The number of cartilage cavities in the newly born child is three or four times greater than in the fœtus, whilst in adults it is scarcely half as great as in the new-born child. In adults the cells are arranged more in groups than in newly born children, and in these more than in the fœtus.

As regards the growth of permanent cartilage in length and thickness, but little is positively known. It is impossible to admit that isolated cell formation in the interior of a large cartilaginous mass can cause an increase in its volume.

The result would, however, be different if the process of division were frequently repeated at the surface, or between two definite cleavage planes throughout the entire mass of the cartilage. Phenomena of growth of the latter kind are, as we shall hereafter see, to be very beautifully observed in ossifying cartilage. Whether a deposition of new cartilage on the old is effected by the perichondrium, as some authors suppose, is a matter still requiring further observation. Very recently attention has been drawn by Bubnoff to the fact that cartilage is traversed by vessels, the tunica adventitia of which sometimes undergoes conversion into cartilage. The relations of the walls of the canals traversing cartilage in which vessels run, to the process of growth, it is therefore obvious, also require investigation.

In their early stages of development, reticulated cartilages are hyaline, and they retain this condition up to the third or fourth month of fœtal life. Fibres make their appearance about the fifth month. Here, as in the elastic fibres of connective tissue, the formation of the fibres can only be traced back to a deposit of fine fibres in the matrix.*

CALCIFIED CARTILAGE.—A deposit of the salts of lime frequently occurs in the matrix of hyaline cartilage.

We shall hereafter trace more carefully such calcification of true cartilage

* Rathke, *loc. cit.* Rabl-Rückhardt, Reichert and Du Bois' *Archiv*, 1863, p. 41.

in the embryonic cartilaginous skeleton, as a preparatory stage of intracartilaginous ossification. Calcification of true cartilage also occurs, in which the calcified tissue persists throughout life. Such cartilage was first described with accuracy by J. Müller,* in the cortex of the skeleton of the plagiostome fishes, under the name of tesselated calcified cartilage.

Calcified cartilage occurs also, as shown by H. Müller,† in a persistent condition at the limits of ossification of the embryonic skeletal cartilage, as, for instance, subjacent to the articular cartilages, at the junction of the ribs with the cartilages of the ribs, and at the synchondroses of the vertebræ and pelvis. It is rare for true bones and uncalcified cartilage to enter into direct contact with one another.

Fig. 20.

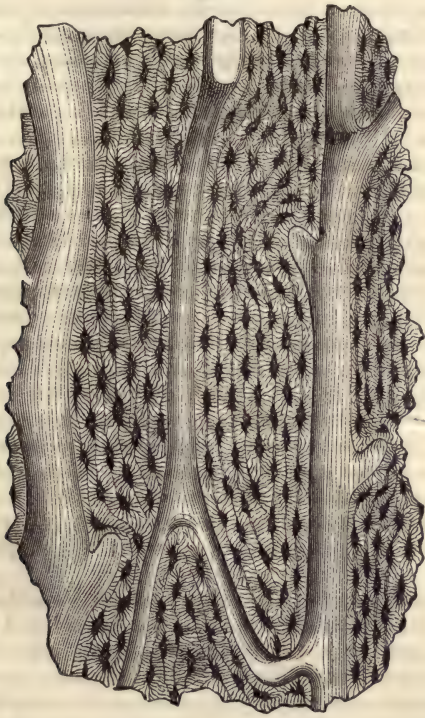

Fig. 20. Longitudinal section of human ulna.

Calcification also occurs in cartilages which, like those of the larynx, begin to ossify with advancing age. In such cartilages it often happens that, notwithstanding parts are found in which both to the eye and touch earthy matters appear to be deposited, examination with the microscope reveals the presence of no true bone, but only of calcified cartilage. Reticulated cartilage only calcifies exceptionally in certain animals, as in the dog.‡

* Poggendorf's *Annalen*, 1836, p. 347.
† *Zeitschrift für wissenschaftliche Zoologie*, Band ix., p. 51.
‡ H. Müller, *Würzburger naturwissenschaftliche Zeitschrift*, Band i., p. 92.

Osseous Tissue.

Osseous tissue forms in man the principal constituent of the bones of the skeleton, and of the cementum of the teeth. This is equally true of all Vertebrate animals. A number of osseous fishes, however, instead of having their skeleton composed of true bone, present a homogeneous or fibrous osteoid substance, traversed by dentine-like tubes which may become actual dentine.* Taking the vertebrate series as a whole, the osseous tissue is widely distributed, since certain parts which are elsewhere composed of soft tissues, as the skin, tendons, and sclerotic coat of the eye, in some animals contain bone. In man, also, osseous tissue occurs in some soft parts as a pathological formation.

Structure of Osseous Tissue.—In a histological point of view, we distinguish in the first place in osseous tissue the matrix and the bone corpuscles. The distinction between these two constituents of bone may be easily perceived on microscopic examination, by transmitted light, of the frequently well-developed thin osseous plates that occur in pathological ossifications, or of the laminæ of the vomer, lachrymal bones, etc., or of fine sections prepared from the larger bones. The corpuscles appear as dark black figures, which consist of a central area, which is either of large size and elliptical, or smaller, and then resembles the section of a bi-convex lens, from which delicate, greatly attenuated, and branched fibres are given off (bone canaliculi). The canaliculi proceeding from different corpuscles intercommunicate,† and thus connect the dark areas with one another.

The dark markings are distributed through a clear matrix (fig. 20); the material in which the corpuscles are situated either appears quite homogeneous in the form of a lamina, or is perforated by variously arranged spaces, which are often so large and numerous that only a network of bony trabeculæ of various thickness is left surrounding them, or the spaces may be of relatively small size, in which case the surrounding substance is split by parallel, straight, or annular lines, into a series of ribbon-like laminæ, to which the corpuscles are attached with tolerable regularity in successive rows.

The dark markings caused by the corpuscles appear equally delicately white and lustrous, if the section is examined by direct instead of transmitted light.

The bone corpuscles and canaliculi were first described by Purkinje and Deutsch.‡ J. Müller§ first pointed out the connection existing between the two, and at the same time expressed his opinion that the entire system of these corpuscles and canaliculi was filled with lime, on which account they were for some time described as corpuscula and canaliculi chalicophori.

The matrix of bone which, as follows from what has been stated above, frequently exhibits a well-marked lamellar structure, is brittle and friable, and confers upon it its peculiar consistence. If a portion of bone be treated with diluted acids, which expel the carbonic acid from its combination with lime, and render the latter as well as the phosphate of lime soluble, the bone becomes soft, whilst it preserves its original form. The softened remains of the matrix represent its organic basis, the so-called *bone cartilage* or *ossein;*

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* Kölliker, *Ueber verschiedene Typen in der Mikroskopischen Structur des Skelettes der Knochenfische*, "On the various Types of Microscopic Structure in the Skeleton of Osseous Fishes." Aus dem ix. *Bande der Würzburger Verhandlungen.*

† Kruckenberg, Müller's *Archiv*, 1849, p. 412.

‡ *De Penitiori Ossium Structura*, 1834.

§ Müller's *Archiv*, 1836, p. 6.

and this, on being boiled with water, is converted into gelatine, though more slowly than collagen is obtained from connective tissue.*

Bones thus softened in acids are well adapted for the preparation of fine sections for the microscope, and present the same appearances as those already described, except that the bone corpuscles now appear by transmitted light more transparent than the matrix.

If lime-containing bones are boiled for a long time, the organic material is in great part or completely removed, and the *earthy matters* of the bone remain behind, still preserving their original form. Chemical examination shows that these earthy matters consist in proportions varying with the animal, and the bone, of a mixture of carbonate of lime, of tribasic phosphate of lime and magnesia, of fluoride of lime, chloride of sodium, and traces of sulphates and of silica. The organic and mineral constituents of the matrix of bone, which are thus capable of being separated from one another, are so intimately blended together both in moist recent and in dried bones, that even with high microscopic powers no distinction can be perceived between them; such, for instance, as a granular precipitate distributed through an organic basis.

It has not been accurately ascertained whether the osseous substance is composed of an intimate mechanical mixture of two molecules, or of a complex double molecule.† In various as yet imperfectly understood diseases (Rachitis, Osteomalacia), the bones lose their mineral matters, and, undergoing other concomitant changes, become soft, flexible, and capable of being cut, whilst the bones of old people, with coincident signs of atrophy (thinning, expansion of the cavities), become more rich in mineral substances, less elastic, and at the same time more brittle.

The coarse morphology of osseous substance, as seen under the microscope, consists then, as already mentioned, of plates, fibre-like trabeculæ, and superimposed lamellæ. The appearances presented in any particular case are dependent upon the osteological importance of the bone examined, upon the direction of the plane in which the section is made, and upon the part of this plane selected for examination.

Osteologists, as is well known, arrange the bones into different groups, as the long or tubular bones, flat bones, and short bones; and structural variations are met with corresponding to these divisions. In the short bones and in the apophyses of the long bones, the osseous tissue forms a thin layer of compact substance on the surface; but in the interior small laminæ exist, inclined at various angles to one another, between which are medullary spaces containing vessels and connective tissue with marrow and fat cells. The substance of the bone consequently here presents a spongy character. In the flat bones, tables of compact substance, corresponding to the two principal surfaces, are superficially placed, between which the osseous substance presents the same spongy character. The compact bony substance is strongest in the diaphyses of the long bones; but even here, in the more internal parts which surround the great medullary cavity, it presents the spongy character which is more conspicuous in proportion as the epiphyses are approximated.

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* Kühne, *Physiologische Chemie*, 1866, p. 391.

† According to the younger Milne Edwards (*Annal. des Sci. Nat.*, 4 S., Tom. xiii. p. 113), different bones yield tolerably constant proportions of ossein and bone earth. But the conclusions to be drawn from all previous analyses of bone are not in accordance with this statement. On feeding animals with unusual diet, as, for instance, withdrawal of flesh from the food of a carnivorous animal, even if the bones are coincidentally supplied with non-nitrogenous material, they become poorer in salts.

On making fine sections of the compact substance of the tubular bones after removal of the mineral matter, some of the finer characters may be very distinctly brought into view. Sections carried perpendicularly to the long axis of the bone exhibit larger or smaller round or slightly oval spaces, which are seldom elongated in a longitudinal direction, but are often bounded by slightly sinuous lines, and represent the transverse sections of the Haversian canals hereafter to be described. Around these the matrix of the bone forms concentrically arranged ribbon-like striæ, which, in a certain focus of the microscope, in the portion nearest to the canals, appear radially striated and somewhat darker than elsewhere. The number of laminæ succeeding one another from within outwards varies, but the smaller canals have fewer than the larger. As many as fifteen have been counted. The system of rings surrounding each space is enclosed by similar rings pursuing a course parallel to the external surface to the bone, so that the latter may be differentiated from the former as being of a higher order; but since the

Fig. 21.

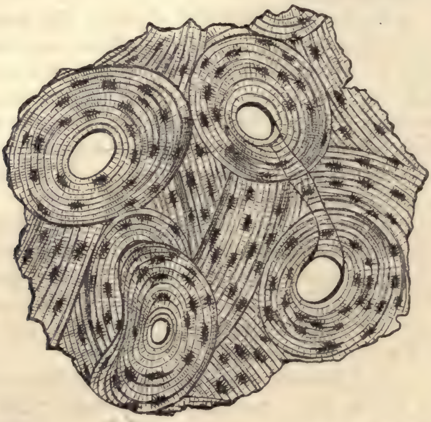

Fig. 21. Transverse section of human femur, deprived of mineral matter by hydrochloric acid.

systems of the first order cease, in some instances nearer, and in others at a point more distant from the surface of the bone, the number of the rings running concentrically with the general circumference of the bone is not constant, but is smaller where the rings of the first order approximate more closely to the surface. Only those which course around the most superficial systems of the first order completely surround the bone.* The spaces which remain between the systems concentric to the Haversian canals in the interior of the bone, and which present areas with three, four, or more angles, with incurved sides, are occupied by an interlamellar mass presenting a similar lamination. The interlamellar systems also, for the most part, run parallel to the surface of the bone; but it may also occur that they run parallel to the two opposite boundaries of the areas, and stand perpendicularly to others; or there may occur in the areas themselves, again, vertices of the systems of rings, which cut the direction of the closed systems at various angles, as shown in fig. 21.

* Tomes and De Morgan, *Philosophical Transactions*, 1853, Vol. i., p. 109.

But we frequently also meet with concentrically arranged systems of the first order, which have become flattened by mutual pressure, and are not separated by any interlamellar substance. The latter seldom occurs in the tubular bones of man, the former commonly occurs in animals.

Frey * calls the connective systems of the first order special or Haversian lamellæ; the others, general or fundamental lamellæ. It is more important to distinguish the three series of Haversian lamellæ, intermediate lamellæ, and peripheric lamellæ.

The open or closed systems of rings seen in transverse sections of bone, are the transverse sections of lamellæ arranged around longitudinal and anastomosing canals, the transverse sections of which last constitute the spaces already described. Of this we may convince ourselves by making longitudinal sections of the long bones (fig. 9), in which the vessels may be seen to form elongated meshes. They either branch at acute angles, or if the branches are more divaricant, they soon follow a less divergent direction, or, which is more usual, they communicate by means of short oblique or rarely transverse branches, and pursue a course that is but slightly inclined to the long axis of the bone. The above-mentioned Haversian or medullary canals, opening upon the external surface of the compact substance, or into the medullary spaces of the spongy substance, are destined for the passage of blood-vessels. The spaces intervening between the Haversian canals are occupied by the ribbon-like longitudinal sections of the lamellæ. Portions of these lamellæ of the compact substance of the long bones may either be splintered off, or they may be obtained by sections made parallel to the surface. With high powers and a good microscope, a sharply defined punctation may be observed in them, besides also an indistinct, dull, veiny appearance, the whole substance being thus divided into a few bright islands.

The punctiform appearance is the expression of small round holes (sections of the bone canals to be hereafter described). The regular rhombs represented by Sharpey,† and observed also by Kölliker,‡ in his earlier preparations, appear to occur only under quite special conditions.

In complete analogy with the arrangement of the Haversian canals and lamellæ of the compact substance of the shaft of the long bones, is that seen in the compact substance of the other classes of bones, when sections are carried through them in various directions, except that the relations are simplified in accordance with the smaller thickness here presented by the compact substance. The lamellæ again in these cases form the extreme boundaries of the bone; and if the thickness of the compact substance is very small, they may even constitute the entire mass of the bone.

The trabeculæ and lamellæ of the cancellous tissue present various forms, and in many instances the stronger trabeculæ are very regularly arranged, so that a kind of fibrillation is exhibited, which pursues a definite direction in regard to the surfaces of the bone examined. H. Meyer § has described such appearances in the bones of the lower extremity of man, and has shown that they stand in a certain relation to the importance of the bone as an organ of support. In the stronger trabeculæ and lamellæ of the cancellous tissue, Haversian canals may be seen with their concentric lamellar systems. In others we obtain, dependent on their more cylindrical or more flattened

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* *Histologie and Histochemie*, 1867, p. 280.

† An illustration of this, after a preparation of Sharpey, may be found in the large *Microscopic Anatomy* of Hassall, Taf. 30, fig. 4.

‡ *Gewebelehre*, 1867, p. 186.

§ Reichert and Du Bois' *Archiv*, 1867, p. 615.

form, and the side from which they are examined, appearances similar to those offered by a flat view of the lamellæ of the compact substance; or else striæ and bands which form the limits of the trabeculæ in regard to the medullary spaces they surround.

We now turn to the consideration of the so-called *bone corpuscles* and their processes. The form of these in the bones of man is elongated and lenticular, and those of animals are for the most part very similar. When seen on the broad surface of the lamellæ, they appear elliptical; but seen on the small transverse section of the lamellæ, they resemble the transverse section of a bi-concave lens. In reference to their position to the lamellæ, they are found at the margins of the latter, arched in accordance with curvature of the surface of the lamellæ where these form small arcs and adhering to their convex surface. In regard to their number, Welcker * counted in each square millimetre of the transverse section of bone 740 on the average in man; the number varying from 780 to 800. Harting gives 910.

From these, as shown in fig. 22, the above-mentioned branched and anastomosing processes are given off in all directions, but especially at right

Fig. 22.

Fig. 22. Bone corpuscles with their processes, as seen in a thin section of human bone.

angles to the lamellæ, and in the direction of the medullary canals. These processes do not, however, run in a single plane, but are much curved, and hence in thin sections of bone, whether transverse or longitudinal, we meet with them cut either transversely or more or less obliquely; and they may either appear still in connection with the corpuscles, or a portion only of their course may be seen; or, lastly, their communication with each other may alone be brought into view (fig. 22). In good sections the fine canaliculi may be followed either to the surface of the bone, or to the medullary

* *Zeitschrift für rationelle Medicin, N. F.*, Band viii., p. 232.

canals and spaces where they terminate by open mouths, or they may reach to the ends of bones invested with cartilage, in which case they terminate in blind pointed extremities.

When the view already mentioned, which led to the terms corpuscles and chalicophorous canaliculi being employed to indicate the lacunæ and canaliculi, had fallen into disrepute because it had been shown by Lessing * that their dark appearance in dry bones on examination with transmitted light, and their white appearance with direct illumination, was to be ascribed to their containing air, and observers were therefore inclined to regard them as constituting a lacunar system, which in the living bones was filled with fluid; the researches of Virchow † again brought into prominence the view that these structures were corpuscles capable of being isolated. Virchow effected the isolation of the bone corpuscles by macerating the lamellæ in hydrochloric acid; but the same result can, according to Förster,‡ be obtained by means of nitric acid. A still better mode of procedure is to boil the bones deprived of lime with hydrochloric acid under pressure. In this mode F. Hoppe § isolated very beautifully the bone corpuscles from the cutaneous plates of the sturgeon. Virchow in the first instance believed that, in accordance with his views on the nature of the connective tissues, he had in these corpuscles isolated the proper cells of bone; and their isolability in such experiments was supposed to depend upon the great resistance of an imaginary cell membrane to the action of hydrochloric acid. We now know, however, that the isolation of these structures can be effected, not only in dry bones, as Virchow already knew, but also in bones which have been long macerated or treated with strong alkalies,‖ and therefore under conditions which would destroy all soft tissues; hence we must admit, that in these experiments a peculiar dense and resistant layer of the matrix of the bone itself is isolated, which forms the wall of the cavities representing the form of the so-called bone corpuscles and their processes. The observations of Kölliker¶ and of Neumann** have an important bearing on this explanation, since in a similar series of experiments they frequently obtained isolated tubules, simulating the form of the Haversian canals. The question, what is the nature of the contents of these cavities during life? is, as thus broadly stated, not easy to answer.

According to a very recent communication, Klebs †† has convinced himself that their contents in the older bones, even when quite fresh, are of a gaseous nature. He rests his assertion especially upon the dark appearance the bone corpuscles present by transmitted light, either in bones examined in the fresh state or under water; secondly, because by means of an air-pump a large quantity of gas can be obtained from the bones; and lastly, because exposure to a solution of potash, which effects the absorption of the contained air (CO), renders the corpuscles transparent.

The bone corpuscles appear to be destitute of air in those bones only which are in contact with soft parts, or in fœtal bones; in point of

* *Ueber ein plasmatisches Gefässystem in allen Geweben insbesonders in Knochen und Zähnen*, "On the presence of a Plasmatic Vascular System in all forms of Tissue, but especially in the Bones and Teeth." Hamburg, 1846.

† *Würzburger Verhandlungen*, Band i., 1850, p. 193.

‡ *Archiv für Pathologische Anatomie*, Band xviii., p. 70.

§ *Idem*, Band v., pp. 179 and 181.

‖ E. Neumann, *Beiträge zur Kenntniss des normalen Zahnbein und Knochengewebes*, "Essays on Healthy Dental and Osseous Tissue." Königsberg, 1863, p. 42.

¶ *Mikroskopische Anatomie*, p. 83.

** *Loc cit.*

†† *Centralblatt für die medicinischen Wissenschaften*, 1868, p. 61.

fact, it is not difficult to demonstrate in many instances that cell-like structures containing nuclei occupy the lacunæ of bone.*

For observations of this nature the large lacunæ of embryonic bones are well adapted, as are also those which are found in the younger layers of bone that lie immediately subjacent to the periosteal connective tissue investing the bones. Good results may be obtained from bones decalcified with weak acids (chromic acid, or a mixture of this with a little hydrochloric acid), especially if thin sections are tinted with carmine. On the other hand, it is difficult, even after this procedure, in the case of old bones, to recognize with certainty either cells or their remains in the granular masses which occur in the lacunæ, and which were long ago observed by Schwann in decalcified bones.

Sharpey † has described certain fibres which come into view, if we attempt to isolate the lamellæ of a decalcified flat or long bone, as constituting a special morphological constituent of osseous tissue. They run in planes which lie nearly perpendicular to the surface of the lamellæ, and appear as pointed processes projecting from the surface of those lamellæ that have been torn away from their attachments; whilst in the adjoining lamellæ the foramina may be recognized from which these so-called Sharpey's or perforating fibres have been withdrawn. As H. Müller ‡ showed, they occur in man in the bones developed in periosteum, and may there attain a length of as much as three millimetres, whilst their thickness varies from 0·002 to 0·005, sometimes even to 0·015 millimetres.

The perforating fibres are calcified rods, which, prior to the formation of the bone lamellæ they traverse, extend as bridges between the embryonic bone and the surrounding connective tissue, through the formative layers of the bone lamellæ; with increasing thickness of the lamellæ they first elongate and then calcify. When a portion of these fibrous bundles remains uncalcified, they form, according to H. Müller, when the bone is dried, the perforating tubes described by Tomes and De Morgan.

Kölliker § has called attention to the wide distribution of the perforating fibres, especially amongst Fishes.

Development of Bone.—Embryological investigation shows that almost the entire bony skeleton of vertebrate animals is developed from a cartilaginous skeleton which is laid down at an early period. This was originally held to be the mode of development of all bones, till Sharpey and Kölliker demonstrated that several of the cranial bones originated directly from connective tissue. These constitute the investing bones of the primordial skull. It has now been known for a considerable time that both kinds of bone, those developed in cartilage (primordial bones), as well as the investing bones (secondary bones), when once formed, receive fresh accessions of osseous tissue from the periosteal connective tissue, and that they thus increase in thickness. Virchow first pointed out that in these cases the osseous tissue is developed from connective tissue in the same way as in the development of secondary bones.

According to these different processes, three separate modes of development

* Donders, Mulder, *Versuch einer physiologischen Chemie*, p. 595. Kolliker, *Mikroskopische Anatomie*, Band ii. p. 297. Rouget, *Journal de la Physiologie*, 1858, p. 764. Beale, *loc. cit.*, p. 128.

† Qüain's *Anatomy*, sixth edition.

‡ *Würzburger naturwissenschaftliche Zeitschrift*, Band i., p. 296.

§ *Ibid.*, Band i., 306.

of bone may be differentiated, the intra-cartilaginous, the intra-membranous, and the periosteal; but we shall see that in all these cases the osseous tissue originates in an essentially similar neoplastic formation (osteogenous substance), and also that the connective-tissue-like deposit preceding the formation of the several bones probably in all cases proceeds from the same germs; in short, that the above-mentioned differences refer to the place where the bone develops, and to the presence or absence of cartilage, but that the process of osteogenesis itself is essentially the same in all.

In those cases where the form of the future bone is more or less distinctly defined in the embryonic cartilaginous skeleton, it may easily be supposed that the matrix of the bone originates in a metamorphosis of the matrix of the cartilage, and the lacunæ and corpuscles either as outgrowths of the cartilage corpuscles, or by the formation of layers of secondary deposit, traversed by porous canals, occurring in the supposed membrane of the cartilage cells. In regard to the formation of the larger medullary spaces, we must admit a process of absorption of the cartilage, or of the young bone developed from it, with coincident development of the contained material. These statements, which were first advanced as a matter of opinion by Schwann* and Henle,† have obtained general acceptance, and for a long time were believed, in Germany, England, and France, to be in accordance with the direct observations which had been made in ossifying cartilage.‡ This was especially the case in Germany, Kölliker§ having employed rachitic bone as a microscopic object where the mode of conversion of cartilage corpuscles into bone corpuscles, described by Schwann as being analogous to the formation of dotted vegetable cells, may really be distinctly followed; and recently Lieberkühn‖ has investigated the normal ossification of cartilage in a series of papers, and has sought to represent the principal facts in accordance with the statements above made in regard to the transformation of cartilage into bone. Another mode, which has proved to be the correct one, notwithstanding that only a few¶ were inclined to accept it, was proposed by H. Müller** in 1858. It was further pursued by other observers,†† and has led to the establishment of the essential facts to be now mentioned regarding the ossification of cartilage.

The ossification of those parts of the skeleton which are originally cartilaginous, proceeds, as is well known, from certain points, called points or centres of ossification. In these there appear in the first instance tubes (cartilage canals) filled with a soft cellular mass, into which blood-vessels, springing from the perichondrium, may be traced (medulla of cartilage).

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* *Mikroskop. Untersuch.*, etc. Berlin, 1839, pp. 35 and 115.

† *Allgemeine Anatomie*, 1841, p. 831.

‡ See for the historical details of the subject the paper by H. Müller in the *Zeitschrift für wissenschaftliche Zoologie*, Band ix., p. 147, *et seq.*

§ *Mittheil. der Zürich Naturforsch. Gesell.*, 1847, Nos. 11 and 12; and Froriep's *Notizen*, 1848, p. 120.

‖ Reichert and Du Bois' *Archiv*, 1862, p. 702; 1863, p. 614; 1864, p. 598; 1865, p. 404.

¶ E. H. Weber, Ausg. v. Hildebrandt's *Anatomie*, 1830, p. 334, u. d. f. Sharpey, Quain's *Anatomy*, fifth edition. Bruch, *Denkschr. d. schweiz. Naturf. Ges.*, Band xi. Baur, Müller's *Archiv*, 1857, p. 347.

** *Zeitschrift für wissenschaftliche Zoologie*, Band ix., p. 145.

†† Gegenbaur, *Jenaische Zeitschrift für Medicin und Naturwissenschaften*, 1864, p. 343; 1866, pp. 54 and 206. Landois, *Centralblatt für die Medicin. Wissenschaften*, Berlin, 1865, Nos. 16, 18, and 32; *Zeitschrift für wissenschaftliche Zoologie*, xvi., p. 23. Waldeyer, *Ueber den Ossifications-process*, *Archiv für mikroskopische Anatomie*, Band i., p. 354.

These canals lead to those parts where, in consequence of the deposition of the salts of lime in the matrix of the cartilage, the white appearance and firm consistence of bone are first observable, and form large irregularly dilated spaces, which are also filled with medullary matter containing blood-vessels. These spots, traversed by dilated canals, lend support to and confer firmness upon the remains of the cartilage, which has now in great part apparently undergone absorption, and is thoroughly impregnated with

Fig. 23.

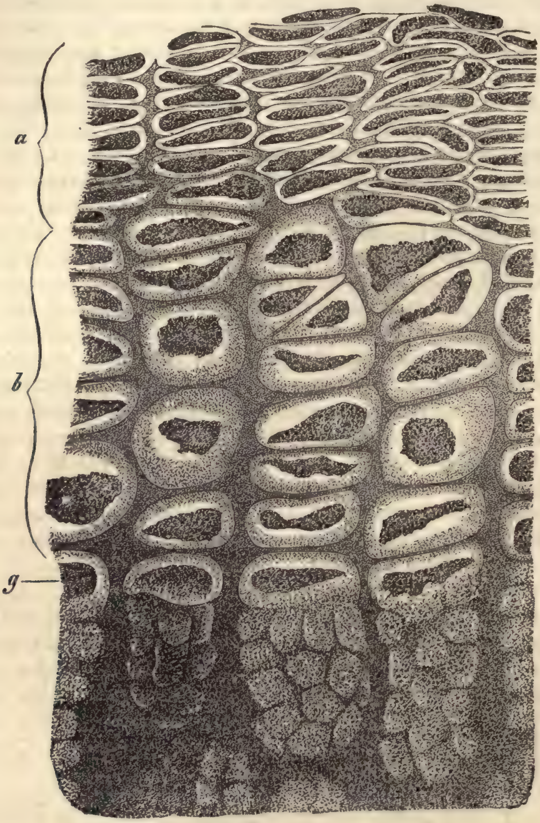

Fig. 23. Longitudinal section carried through the line of ossification of a tubular bone. From a human embryo.

granular deposits of lime. In the neighborhood of these spots the cartilage appears transparent and composed of large clear cells separated from one another by only a small portion of matrix. When a more careful examination is instituted, it is observable, however, that the limits of the cavities filled with medulla, and the large-celled cartilage region, on the one hand, and the limits of the calcified trabeculæ and the large-celled cartilage region on the other, do not coincide; for the calcified portion may be followed beyond the limits of the medullary spaces, and terminates in the form of fine processes in the larger trabeculæ of the matrix of the still unpenetrated

cartilage. The cells at the limits of the latter appear to occupy the tubular extremities of the calcified tissue, and there first come into contact with the medulla. Such are the processes in cartilage that precede the formation of bone. Osseous tissue is only developed in those parts where medullary substance has been first formed, and, indeed, upon its surface, being superimposed upon the previously calcified cartilage. In regard to this point, however, a fuller description will hereafter be given. It is not difficult to see these phenomena in the centres of ossification of the short bones, or in the diaphyses of the long bones. The centres of ossifications of the epiphyses which appear at a later period are also exceedingly well adapted for observations of this kind. The embryos from which the preparations are made ought previously to be macerated in chromic acid, or still better, in Müller's fluid. The most instructive specimens are furnished by keeping the preparations for a somewhat longer time in the latter fluid till they can be cut with facility, and then staining them with carmine.

The changes described gradually extend from the centre of ossification into the adjoining cartilage. Longitudinal sections through the diaphyses of fœtal bones, which display the margins undergoing ossification, are best adapted for microscopic investigation. The appearances presented by such a longitudinal section, if it contains all the parts undergoing change from the still unaltered cartilage to completely formed bone, are the following (fig. 23). Immediately below the cartilage exhibiting the characters of fœtal cartilage, as it appears previously to ossification, there follows a layer of cartilage (*a*) in which the cells lie more closely compressed together, and present a definite arrangement. They form longitudinal rows. In these rows the cells appear as plates flattened in the direction of the long axis of the bone, superimposed upon one another, so that a transverse section made from this region presents some similarity to that of the free surface of the articular cartilages, or that exhibited by other cartilages in the layer immediately beneath the perichondrium. These long rows of flat cells are further characterized by the circumstance that they are often clavate, and intercalate with one another alternately, with their pointed extremities directed in opposite ways.* It is moreover not difficult to convince one's self that these rows of cells originate in continuous processes of fission; and in regard to this point the preparations are very instructive that were examined and described by Aeby, showing that the club-shaped cells develop from the transverse fission of elongated cells, the daughter cells becoming placed alternately one above the other. The several long rows of flat cells are not all arranged at equal distances from one another, but are divided into variously sized vertical groups by strong trabeculæ of the matrix.

To the well-characterized region of flattened cells, arranged in vertical rows, there succeeds near the line of ossification a second region (*b*), in which clear and remarkably large cells containing beautiful spherical nuclei are found. The larger size of these cells, in comparison with those contained in the region just described, is to be attributed chiefly to the increase of the diameter coinciding with the longitudinal axis of the bone. This region contains in the same area a much smaller number of cells than even the primary cartilage lying over the region where they are arranged in vertical rows. Examined with the naked eye, the region of large cells seen in longitudinal section in fresh fœtal bone appears clearer and more transparent than any other part. This region presents a great similarity to that stage of fœtal cartilage in which the cells are still capable of being easily isolated.

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* Aeby, *Zeitschrift für rationelle Medicin*, 3 R., Band iv., p. 38, u. d. f.

Between the large transparent cells such strong trabeculæ of the matrix alone intervene as run parallel to the longitudinal direction of the bone, and between which the cells lie in single or more frequently in multiple rows. Where these trabeculæ are absent, the cells appear to be in direct contact with one another. Even then, however, when the cells have become somewhat shrivelled, a very delicate structure may be distinguished, formed by the presence of small quantities of the matrix intervening between each of the vertical rows. The septa intermediate to the cells in the latter case are arranged like the steps of a ladder (see the illustration) between the adjoining longitudinal trabeculæ. Still more internal to the region of large cells, the thicker vertical trabeculæ become the seat of the deposit of the lime salts, in the form of small granules or confused masses on their internal surface, and at the same time they become somewhat thicker. We then reach the region of calcified cartilage, which, according

Fig. 24.

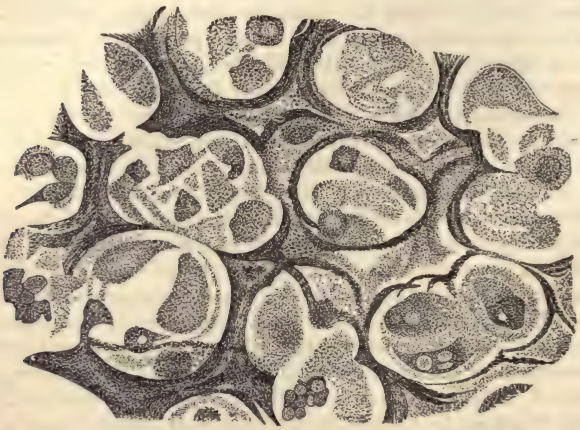

Fig. 24. Transverse section through fœtal cartilage in which ossification has commenced.

to H. Müller,* usually precedes the true process of ossification. A very beautiful mode of supplementing the images hitherto only seen in longitudinal section, and which have been best described by Waldeyer,† is that by which transverse sections are examined that are successively carried through the several regions above described.

The appearances presented by transverse sections of the calcified cartilage are especially worthy of notice. In these, calcified rings surrounding one or several of the large cells, and characterized by their granular or cloudy appearance, come very distinctly into view. If the transverse section approximates nearer to the bone, the calcified rings increase in thickness, and still lower down the cells which occupy the calcified rings become smaller, more numerous (fig. 24), and more strongly granular. Beneath these cells we find masses of protoplasm often of considerable size, containing two or more nuclei, together with a great number of small nuclei.

* *Loc. cit.*, p. 157.
† *Loc. cit.*, p. 359, v. Taf. 22, fig. 2.

The many-nucleated cells have been rightly associated by Gegenbaur * and Waldeyer, † with the myeloplaxes described by Robin. ‡ The selection of successively lower planes for the transverse section thus leads from the large-celled region, the calcified rings remaining without essential change, to a plane in which proliferated cells appear between the calcified trabeculæ. This also immediately becomes evident if we return to the examination of a longitudinal section.

The appearance presented by a longitudinal section is further rendered very remarkable by the circumstance that the elongated spaces bounded by the above-described calcified trabeculæ, suddenly, at a tolerably well-defined limit (*g*, fig. 23), change their contents from large cartilage cells to a material of a different nature. This consists of granular cells that lie closely compressed against the cartilage. These cells are provided with a variable number of longer or shorter processes, which, however, can only be well seen in preparations that have been teased out with needles, or pencilled out with a brush. If we follow up the trabeculæ surrounding these masses in the direction of the cartilage, we shall see that the granular cells, accumulated where the cartilage commences, form an epithelium-like layer investing the surfaces of the expanded prolongations of the vertical trabeculæ, whilst the middle part of the contained mass is occupied by delicate fusiform or stellate cells, amongst which, however, small roundish coarsely granulated cells are distributed. In this last tissue well-developed blood-vessels are clearly visible.

Thus in the cavities of calcified cartilage there appears in the first instance a new soft material composed of numerous cells, of which the superficially situated are differentiated from those that occupy the interior.

The question now arises, from whence do these tissues originate? It is to be remarked that the limits between the large-celled region of the cartilage, and the subsequently formed contents of the spaces bounded by the calcified trabeculæ, are very sharply defined in all the preparations I have examined. I have never been able to discover any transitional stages between the large clear cartilage cells and the dark coarsely granular cells which suddenly make their appearance. Such transitional stages might, however, be expected to occur frequently if the cartilage cells constituted mother cells, giving origin to those of the medulla by fission. However high, therefore, may be the authorities by which the latter view is supported, I must still doubt its accuracy. It is indeed conceivable that processes of division may here occur with such rapidity as to be concealed from the eye of the observer, and thus lead us to grant the development of the medulla from the cartilage cells, as a convenient theory, though unsupported by direct observation. We are certainly, however, not compelled to admit this view, since there is no difficulty in supposing the medulla to shoot into the cartilage from the same surface as that from which the blood-vessels emanate. This last view is especially supported by the circumstance that, as we shall see, an analogous productive activity must necessarily be attributed to the medulla, and will hereafter be traced in it.

The productive activitity of the cartilage cells appears to me to cease at the limits of the flat-celled region. The large vesicular cells which extend from this point to the plane of ossification may frequently be seen where the medulla commences, in a state of finely granular atrophy, similar to that of the cartilage matrix itself, so that only the remains of these cells are found in the medulla.

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* *Loc. cit.*, p. 349.
† *Loc. cit.*, p. 362.
‡ *Journal de la Anatomie, de la Physiologie*, Tom. i., p. 88.

The view here given at length must not be confounded with the statements made by Henke,* respecting the origin of the cartilage elements at the plane of ossification, according to which even the vertical rows of cells contained in the medullary spaces are formed at the expense of blood-corpuscles that have escaped from the vessels.

We have already pointed out that coincidently with the change that occurs in the nature of the material occupying the interspaces of the calcified trabeculæ a differentiation of its constituent cells may be observed to take place into an outer and an inner layer.

The granular cells of the outer layer were first described by Gegenbaur,† who applied the term *Osteoblasts* to them, whilst he considered the more transparent internal tissue to be the proper medulla in an early stage of development. The osteoblastic layers are found in the cavities already described (primary medullary spaces), sometimes forming thin and sometimes thicker layers, interposed between the remains of the original cartilage on the one hand, and the vascular medulla on the other.

The formation of the osteoblastic layer constitutes the immediate precursor of true osseous tissue. The latter occurs in the walls of the primary medullary cavities, at some distance from the margin of the cartilage, and when first seen constitutes a thin, lustrous, highly refractive lamella, in which the peculiar stellate form of the bone corpuscles is already visible. Wherever this tissue is formed, osteoblasts have previously been deposited in layers, and just as in the first instance the remains of the trabeculæ of the calcified cartilage, so at a later period the young bony tissue deposited on the surface of these is again covered by a layer of osteoblasts separating it from the medulla.

All the peculiarities above described, with the above-mentioned exception of the relation of the cartilage cells to the medulla, may be traced with perfect accuracy.

It is more difficult to ascertain the relation of osteoblasts to newly formed bone.

Gegenbaur supposes the osteoblasts to form a hardening secretion, in which they are subsequently themselves enclosed, appearing in the form of the stellate bone corpuscles. Waldeyer has drawn attention to the difficulties of this explanation, and has sought to show that the osteoblasts are constantly converted into bone in a lamellar fashion, whilst new layers are constantly being differentiated from the medulla. In undergoing this change the osteoblasts assume a smoother and more homogeneous appearance, and, whilst their nuclei break down and vanish, become hardened into the matrix of bone; in some of them, however, only the external portions undergo this fusion and calcification, the inner portion with the nucleus remaining as bone cells enclosed in a stellate cavity. The latter explanation corresponds with much greater exactness than the former to the facts that have been observed.

Before discussing this subject further, we shall now proceed to show that the formation of bone in periosteal tissue and in investing bones occurs under the same conditions as those of which we have acquired a knowledge when considering intra-cartilaginous ossification. In reference to the latter it must still be remarked that although the exposition given above has been especially derived from the examination of human embryos, it has also been observed in allied animals.

In describing the processes taking place at the ossifying surface of the diaphyses, we have already become acquainted with those which determine

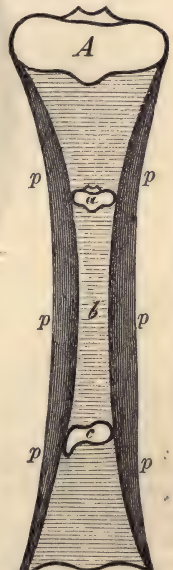
* *Zeitschrift für rationelle Medicin*, 3 R., Band xviii., p. 61.

† *Loc. cit.*, p. 360.

the increase in length of the tubular bones. Their *increase in thickness* is dependent upon the processes we are now about to describe. Grew * and Havers † were the first to point out that a deposit of new bone takes place upon that already formed from the periosteum, but it was the researches of Du Hamel ‡ that led to the general recognition of the fact.

In the development of the tubular bones, the process of periosteal ossification may even precede the intra-cartilaginous. In such cases the cartilage, either in a pure state, or perforated by canals, and calcified, and in the preparatory stage of intra-cartilaginous ossification, becomes enclosed in a tube of osseous tissue.§ In certain animals, medullary substance replaces cartilage in the middle portion of the bone; whilst in other animals, and also towards the apophyses of the bones in the former instances, a few intra-cartilaginous bony trabeculæ are developed, which become altered to the periosteal tube. In a few cases, as for example in sections of the tubular bones of the extremities of the adult Proteus, we find an osseous tube composed of a few periosteal lamellæ, the cavity of which is filled with true cartilage that has undergone calcification.

Fig. 25.



An easily intelligible diagram, showing intra-cartilaginous and periosteal ossification proceeding together, as occurs in the formation of the long bones of the higher vertebrata, is exhibited in the adjoining figure (fig. 25), by H. Meyer; ‖ *a b c* indicate the bone of an infant; A *b* C the form which the bone of the adult acquires by intra-cartilaginous growth, whilst its increase in breadth results from the periosteal deposit *p*. The ossific capacity of the periosteum causes a reproduction of bone to occur if the latter be resected from its investing periosteum.¶ Upon this circumstance depend the osteo-plastic processes that have been observed after the transplantation of excised portions of periosteum, and which are especially active in young animals, and to some, though a smaller extent in adults.** The peculiar histological processes occurring in periosteal ossification have been fully discussed by Virchow, and more recently by Gegenbaur, Waldeyer, and Landois, in the works above mentioned. The processes are more simple in animals where successive lamellæ only are deposited, but more complicated when Haversian canals are developed, with their concentric systems of lamellæ.

We shall in the first instance discuss the processes which occur in the latter case, and for this purpose a transverse section carried through one of the bones of the forearm of a human embryo at the fifth month, invested with its periosteum, may be advantageously studied (fig. 26). With low microscopic powers we obtain from this the very instructive appearance which is diagrammatically represented in fig. 26. The diagrammatic character of the illustration,

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* *English Academy*, 1681.
† *Osteologia*, etc. Frankfurt and Leipzig, 1692.
‡ *Mémoires de l'Académie de Paris*, 1742, p. 354; 1743, pp. 87, 111, and 288.
§ Dugés, Rathke, Bruch, Reichert, H. Müller, *loc. cit.*, p. 193.
‖ Müller's *Archiv*, 1849, p. 292.
¶ Heine, Gräfe and Walther's *Journal*, 1839, p. 513, and many recent observers.
** Ollier, *Journal de la Physiologie*, Tom. ii., pp. 1 and 169.

however, relates only to the tissue elements introduced into it; the dimensions of the several layers being correctly indicated.

A homogeneous smooth lamina may here be seen in the first place constituting the outer layer of the periosteum, consisting, as appears from its examination with high powers, of decussating fasciculi of connective tissue divided in various directions in the section. Between the fibrillæ fusiform cells with elongated nuclei are distributed. To this external layer of the periosteum succeeds a tolerably broad internal layer *b* (Cambium),* which with low powers is distinguished by its containing a large number of small

Fig. 26.

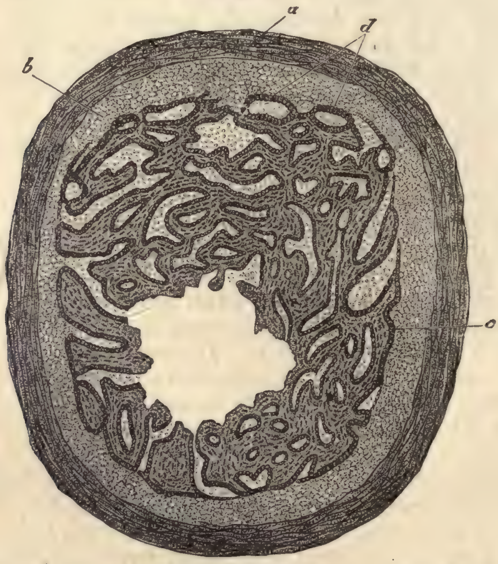

Fig. 26. Transverse section through one of the bones of the forearm of a human embryo, at the fifth month. (Half diagrammatic.)

round bodies that appear to be imbedded in the meshes of a fine plexus, and confer upon it a granular aspect. If we examine these layers separated from one another under high powers, and combine therewith the results obtained from the investigation of preparations teased and pencilled out, we shall observe in the first place that the granular appearance depends upon the presence of small roundish nucleated cells. The cells give off a variable number of fine processes from their periphery, which join the reticulum; the latter possesses a structure which it is difficult to unravel, for we do not find in it the well-developed stellate cells present in the reticulum of the lymphatic glands, but flattened cells that are finely granular in the portion lying next to the nucleus, and at various points, but frequently only at the two opposite poles, give off long homogeneous processes. In very many instances the isolated cells become continuous at their periphery with a fine trabecular trellis-work of wing-like form connected with other fine and smooth trabeculæ traversing the reticulum.

On the internal surface of the second layer of the periosteum which we

* Billroth, *Archiv für klinische Chirurgie*, Band vi., p. 723.

have just described, there follows a third layer *c*, which contains large granular cells exactly comparable to the above-mentioned osteoblasts, and forms an epithelial covering continuous with the periosteal investment of the bony trabeculæ. By teasing out the specimen with needles, it may be demonstrated that the apparently spherical cells are here also provided with numerous fine homogeneous processes, which on the one hand penetrate into the already described reticulum, or on the other hand extend to the surface of the bone, into the substance of which they pass without interruption.

The cellular investment of the osseous trabeculæ is, however, not continuous, since between the separate granular osteoblasts the somewhat expanded processes of the before-mentioned reticulum penetrate and proceed directly to the surface of the bone, into the matrix of which they pass without apparent interruption. In correspondence with the larger size of the osteoblasts, the meshes of the reticulum of bone are likewise enlarged.

Such are the appearances presented by a transverse section in which fully formed bone, layers of osteoblasts, and small-celled and fibrillar periosteal layers immediately succeed one another in parallel series.

This, however, can be observed only in a few places. The external form of the transverse section shown in fig. 26 is conformed to the shape of the external and internal limits of the fibrillar portions of the periosteum. The internal surface of the bone everywhere invested with osteoblasts is, on the other hand, irregularly bulged and dentated, whilst the arcuate boundaries of the cavities occurring in the bone project towards the periosteum. From the arches of the completely developed bone other arches spring, which, exclusively composed of osteoblasts, are directly continuous with the osteoblasts investing the bony trabeculæ. The last-named arches are either entirely closed externally, forming completely differentiated rings of osteoblasts, or we may observe two arched processes inclined to one another, constituting the commencement of a future ring. These incomplete arches then enclose a part of the already described small-celled second layer of the periosteum, the enclosed and the unenclosed portions being continuous through the orifice left in the crown of the arch, and in the first instance presenting identical characters. We have thus acquired a knowledge of the first formation of the Haversian system and canals, as well as of the medulla primarily contained in the latter. In passing from without inwards we may recognize all stages of transition from the first formation of the projecting osteoblastic arches, and from the first incomplete arches projecting from the bone, and closed only by an osteoblastic layer, to the completely closed lamellæ of bone. All these newly formed rings and arches of bone are invested on their inner surface with osteoblasts, and upon their external surface also, especially where they are in contact with the periosteum. The tissue enclosed by the newly formed bony arches soon becomes more transparent, highly vascular, and then contains small roundish cells which appear granular, together with others that are more transparent, elongated, and fusiform, resembling those which are met with in young connective tissue. In the mode illustrated by the example we have adduced, the process of formation may be followed in the later stages of development, during the period of increase of the bone in thickness.

Since the great medullary cavity occurs as a secondary formation in the tubular bones, in consequence of a great part of the bone developed by intra-cartilaginous ossification having undergone re-absorption, we find in adult bones that the medullary cavity in the middle portion of the shaft is bounded for the most part only by the intercalated or Haversian systems of bone which have been formed by periosteal osteogenesis.

As in the intra-cartilaginous mode of ossification, so also in the periosteal form, a continuous layer of osteoblasts may be observed to constitute the immediate precursor of the formation of the osseous tissue.

It still remains to be noticed, that, in transverse sections made as before, strong fibrous bands may be followed, pursuing a radiating course through all the layers of the periosteum, from the exterior to the bony trabeculæ; these are continuous with the fasciculi of the outer layers of the periosteum, appear to be quite independent of the rings and arches of osteoblasts, and are to be regarded as the earliest condition of the perforating fibres of Sharpey.

If we examine the longitudinal section of one of the long bones of an aborted embryo or very young child, in the same way that we have already examined the transverse section, we shall see stretching over spaces of considerable extent in the periosteum, near the surface of the bone and imbedded in the small-celled layer of the periosteum, a layer of well-defined osteoblasts, arranged longitudinally in a striated manner, in which the processes that take place are less distinctly visible than in transverse sections, and, indeed, become intelligible only by comparison with the latter. The appearances presented by such longitudinal sections are, however, very similar to those which are obtained from the early stages of development of the so-called investing bones.

The ossification of the investing bones, the so-called *intra-membranous ossification* was first distinguished from the intra-cartilaginous by Nesbitt,* and subsequently by Sharpey.† The description of intra-membranous ossification given by Sharpey was substantiated by Kölliker, and in consequence obtained general acceptance. The finer details of this mode of ossification may be found in the recent observations published by Lieberkühn‡ and Waldeyer.§

The expanded portion of the occipital bone, the parietal and frontal bones, the squamous portion of the temporal bones, the ossa Wormiana, and the facial bones are all developed in membrane. The clavicle was included in the number of these bones by Nesbitt and Bruch, but incorrectly, as was shown by H. Müller‖ and Gegenbaur.¶ The development of those bones which are not formed in cartilage proceeds, however, like them, from one or from a limited number of points. The tissue in which these bones originate exhibits a great similarity to that which has been already described as the second layer of the periosteum, or as constituting the young medulla within the rings of well-defined osteoblasts. In this tissue there first appear at the points from which the ossification commences, small thin trabeculæ, which unite in a plexiform manner, and this differentiation of tissue progressively extends in a radiating direction. The spaces enclosed by the anastomosing trabeculæ are wider towards the periphery than at the point from whence the ossification commenced. Towards the periphery the trabeculæ are also thinner, and form finely pointed and radially directed processes, and after assuming this arrangement become calcified and converted into bone. If we examine such trabeculæ before they have undergone ossification, it will be seen that they consist of numerous cells, elongated in accordance with the long axis of the trabeculæ. These cells appear strongly granular in their

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* *Osteogeny*, etc., translated by J. C. Greding. Altenburg, 1753.
† Quain's *Anatomy*, by Quain and Sharpey, fifth edition.
‡ Reichert and Du Bois' *Archiv*, 1864, p. 610.
§ *Loc. cit.*, p. 368.
‖ *Loc. cit.*, p. 201.
¶ *Jenaische Zeitschrift*, 1864, p. 1.

thicker median portion, and contain a round nucleus. They resemble the osteoblasts found elsewhere, but are elongated to a still greater extent in one of their axes. Between these cells with their interlacing processes, fibres extend, either singly or in small bundles, in association with which the processes of these cells run, so that the several trabeculæ present collectively the appearance of connective tissue at a certain stage of its development. At a period immediately succeeding the formation of this fibro-cellular material constituting the rudiment of the secondary bones, we may trace in the

Fig. 27.

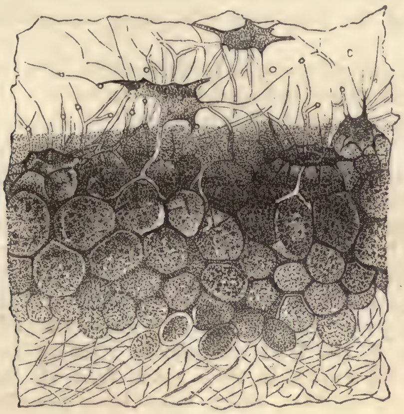

Fig. 27. Bone trabeculæ with osteoblastic layer, from the parietal bone of a human embryo, at the fifth month.

most beautiful manner, in preparations which have been teased out, how the whole deposit calcifies and acquires the character of osseous tissue. Each newly formed trabecula of bone is invested on its surface with a layer of osteoblasts, and in proportion to the increasing thickness of the trabeculæ the investing layers of osteoblasts assume the character of an epithelial layer (fig. 27), as it presents itself in the primary medullary spaces of the long bones, or in the material in which the Haversian canals are about to form. The trabeculæ of a secondary bone, proceeding from different centres of ossification, unite with one another at a later period. They form broad transverse trabeculæ, parallel to the surface of the bone on which new layers are deposited, causing the bone to become thickened, as in the periosteal increase of bones developed from cartilage.

When we thus follow the three above-named modes of development of osseous tissue, it is seen that we meet only with variations that gradually pass into one another.

In the case of intra-cartilaginous ossification, the substitution from the first of a new tissue for the cartilage which subsequently calcifies, removes the difficulty of explaining the molecular difference between the matrix of cartilage and the organic matrix of bone which was formerly experienced, when the impregnation of cartilage with salts of lime was regarded as the essential condition of the ossifying process.

There further occurs a complete agreement between the origin of the first rudiments of true bone and the primary layers by which growth is effected.

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In reference to the latter, it is found that they only partially succeed one another in a centrifugal direction, leading to a change of form in the bone, whilst they are chiefly superimposed centripetally towards the cavities which were bounded by the first deposits, leading probably in all instances to a relative increase or diminution of the sclerosed as well as of the soft parts contained in a given area. We do not possess any macroscopic observations which tend to the supposition that, in bone once formed, growth may occur by intus-susception. The microscopic observations instituted in reference to this point are open to various interpretations, and we shall only remark here that objections have been recently raised against the well-known experiment of Hunter, negativing an interstitial increase of bone, because two orifices made in the shaft of the long bone of a young animal did not retreat from one another.

We have seen in our microscopic investigations how intricate the relations are in regard to centrifugal and centripetal deposition of new bone, and how the formerly described periosteal development of the complex long bones, in which the greater part of the intercalated and investing lamellæ and the most external Haversian lamellæ originate apparently by centrifugal deposition, whilst the internal Haversian lamellæ originate in centripetal deposit.

If sections are made of growing bones decalcified with chromic acid, or if bone be macerated in Müller's fluid, which however does not facilitate their section, and are then rubbed down with this fluid and treated with carmine, the osteoblastic layers and the immediately adjacent youngest layer of bone acquire an intensely red color, whilst the remainder of the osseous tissue, with the exception of the bone corpuscles, remains uncolored. We thus obtain specimens very similar to those made from the bones of animals fed for a short time with madder, which have been described and depicted by Tomes and Hassall.*

It is well known that it has been sought to draw some definite conclusions respecting the process of absorption and regeneration of bone, from the observation of the laminated coloration of the osseous tissue occurring after the use of madder, on the ground that such colored parts represent the most recently formed layers.

It is well worthy of notice that the experiments with madder first instituted by Du Hamel,† and repeated at a later period by Flourens,‡ at a time when very little was known respecting the histological process of ossification, and which were certainly unjustly brought into discredit by Gibson,§ have again been recently taken up by Lieberkühn. The above-mentioned analogies, and the more delicate histological relations occurring in the formation and resorption of osseous tissue, still require to be subjected to a systematic investigation.

Contents of the Bone Cavities.

The medulla which occupies the central cavity, and the large medullary spaces especially found in the fully developed long bones, is composed of a delicate connective tissue traversed by vessels, and containing numerous fat cells, to which last its yellow color is due (yellow medulla). This fatty medulla cannot in any way be compared with the above-described young

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* *Loc. cit.*, plate 30, fig. 6.

† *Mémoires de l'Académie de Paris*, 1742, p. 354; 1743, p. 138.

‡ *Annales des Sciences Naturelles*, série, 2, xiii., p. 103.

§ Meckel's *Archiv*, Band iv., p. 482.

medulla of bones in process of formation; it represents a stage of development of the former which has progressed in another direction, and no osteogenic activity can be attributed to it.

The medullary spaces of the spongy substance, on the other hand, contain a reddish mass traversed by numerous blood-vessels (red marrow), and presenting, with but few fat cells, a large number of granular cells similar to those that are found in the embryonic medulla. Amœboid movements occur in the cells of the bone medulla analogous to those seen in the colorless blood cells;* in the latter localities the large many-nucleated masses of protoplasm are found described by Robin† under the name of Myeloplaxes, and which are most abundant in the external layers of the medullary masses occupying the bone cavities. Bredichin‡ is of opinion that the colossal cells (Myeloplaxes) proceed from the bone tissue itself, *i. e.*, from the bone cells with coincident absorption of the matrix, and that this conversion is continuous with the formation of medullary canals during the growth of the bone. As the different sized medullary spaces of the bone are continuous with one another, so do also the yellow and red medullæ gradually pass into one another. In the skeleton of birds many bone cavities morphologically comparable with the medullary cavity of other animals are filled with air instead of medulla.

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* Bizzozero. Rovida, *Wiener Sitzungsberichte*, Band lvi., p. 608; and *Centralblatt für die medicin. Wissenschaften*, 1868, p. 245.

† *Journal de l'Anatomie et de la Physiologie*, 1864, p. 88, plates 1, 2, and 3.

‡ *Centralblatt für die medicin. Wissenschaften*, 1867, p. 563, provisional communication.

CHAPTER III.

THE GENERAL CHARACTERS OF THE STRUCTURES COMPOSING THE NERVOUS SYSTEM.

By MAX SCHULTZE.

The structural elements of the nervous system, speaking generally, are of three kinds. To the conduction of nervous influence the *nerve fibres* are subservient, which not only compose the nerve trunks, but also constitute an essential part of the substance of the central organs. At the peripheric extremities of the majority of these fibres peculiar *terminal organs* are found, representing the second structural element of the nervous system; whilst the third is formed by the peculiar structures situated at the origin of each fibre in the nerve centres. These are the *ganglion cells.* Our subject therefore is naturally divided into a consideration of

1. The nerve fibres.
2. The peripheric terminal organs of the nerves.
3. The centric organs of the nerve fibres.

The Nerve Fibres.

The nerve fibres form the chief constituents of all nerve trunks, in which they are mingled with connective tissue and blood-vessels; they also enter largely into the composition of the central organs, forming not only the whole of the white substance, but constituting a considerable portion of the gray matter. They are in part very simple, but in part also very complex structures, and there are consequently several varieties of them. The primitive nerve fibrils present the simplest form. These are the very fine threads which lie on the extreme verge of microscopic mensuration, and are only rendered visible with powers of effecting an apparent enlargement of from 500 to 800 linear. They are moderately frequent in the central organs and in the neighborhood of the peripheric terminations. In such fibres as these no internal structure can be detected by the microscope. Their nervous nature is, however, placed beyond the possibility of question by their connection with ganglionic cells, and by the evidence of their issuing from thicker nerve fibres. When fresh, it is very difficult to isolate them, but this may readily be effected in preparations that have been carefully hardened. On treating the fibrils with watery solutions of different salts in certain degrees of concentration, and with solutions of chromic and perosmic acids, besides being hardened, they undergo during the first few hours a process of partial imbibition, occasioning the appearance of varicose enlargements, having a more or less regular fusiform shape, and these subsequently, by further imbibition, increase in size and number until at length the fibre becomes unrecognizable and disappears.

A second kind of fibre very commonly met with in the central organs, is distinguished from the foregoing by its greater thickness. Such fibres are very delicate, transparent, and perishable, of albuminous composition, and only isolable for short tracts. Their diameter is very various, amounting only to a few micromillimetres. Speaking generally, they are the fibres

which have been termed naked axis cylinders. The thicker they are the more easy is it to distinguish their internal structure. This presents a more or less well-marked longitudinal striation, resulting from a fibrous differentiation of the substance of the fibre, and from the presence in all probability of an interfibrillar finely granular material. It is most easy to discern that they are composed of fibrils in the thick-branched processes of the large centric ganglion cells, which Deiters proposed to call *protoplasmic processes*, a name for which I substituted the term *ramifying processes.** More-

Fig. 28.

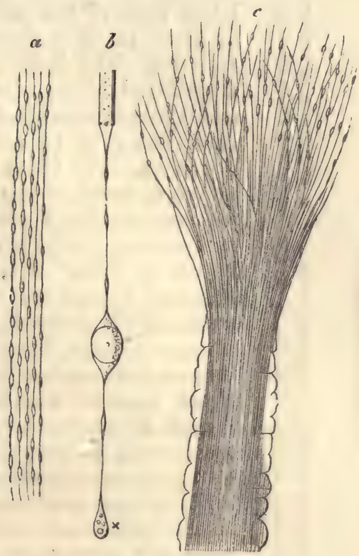

Fig. 28. Primitive nerve fibrils. *a*, from the nervous fibre layer of the retina; *b*, from the external granule layer of the retina, showing at *x* a larger varicosity, resulting from imbibition; *c*, from the olfactory groove of the Pike, showing a thick nerve fibre enclosed in a sheath, breaking up into fibrillæ.

over, the axis-cylinder processes even of these ganglion cells and other fibres of the central organs of the nervous system usually regarded as naked cylinders, and believed to run for considerable distances without branching, often present a distinctly fibrillar structure. Their fibrillar character is most distinctly visible at their origin from the ganglion cells, as shown in fig. 29 (at *x x*). I have applied the term "primitive-fibril bundles, or fasciculi," to this second kind of fibre.

Both kinds of fibres, the primitive fibrils and the fibrillar fasciculi, may become invested with a medullary sheath, as in the adjoining figure (at *a*), and thus become converted into a third form of nerve fibre, *the medullated.* The medullated fibres therefore consist essentially of two constituents, a cortex or sheath of medullary nerve substance, and an axial fibre or axis

* See Deiters' *Researches on the Brain and Spinal Cord*, Brunswick, 1865; and my Preface to his Book, pp. xv.–xvii.

cylinder, which is either a primitive fibre or a bundle of fibrillæ. The medullary sheath forms a more or less thick investment around the axis cylinder, and consists of an oily substance containing protagon, and capable of powerfully refracting light. It gives to the nerves their characteristic dark strongly defined borders. Considering the great delicacy of the axis cylinder, and the perfectly fluid nature of the medullary sheath, the consistence of these medullated fibres cannot, it is obvious, be very great. In point of fact, the difficulty of isolating the medullated fibre of the nerve centres is quite as great as in the case of the naked axis cylinder. The isolation of unaltered fresh medullated fibres, obtained from the gray and white substance of the brain and spinal cord, can only be accomplished for short distances. The fibres break up into short pieces as soon as the preparation needles are used, partly in consequence of pressure and tearing, but partly also from the imbibition of fluid. Even when the more indifferent liquids are employed, these fragments of fibres rapidly undergo remarkable changes of form, developing knots and swellings on their surface (see fig. 31), and sometimes regular moniliform enlargements, though for the most part such enlargements appear only as irregular varicosities, giving a very characteristic appearance to the fibre. After a short time numerous spherical and short cylindrical curved masses separate from the medullary investment, or from the whole soft fibre, and swim freely in the liquid in which the preparation is contained, constituting the so-called myelin drops (*b*).

Fig. 29.

Fig. 30.

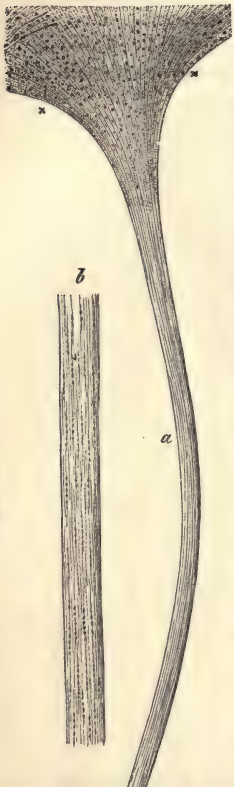

Fig. 29. *a*, axis cylinder, showing its fibrillar structure, at its upper part *x x* originating in a ganglion cell, and at *a'* becoming invested by a medullary sheath. Fig. 30. Naked axis cylinder from the dorsal region of the spinal cord of the Ox. The medullary sheath has been removed.

The medullary sheath, especially where it surrounds the axis cylinder, as a somewhat thicker layer, changes after death, by what may be termed a kind of coagulation, into a granular semi-transparent mass. The changes proceed from without inwards, affecting the homogeneity of the mass, and altering the originally transparent highly refractive fibre in a very peculiar manner (see fig. 32 *d*). The change is accelerated by the addition of water, whilst it is delayed for many hours by immersion in solution of iodine in serum. The addition of a solution of perosmic acid hinders the coagulation of the medullary substance of the nerves in a similar manner, and moreover colors it of an inky black.

The medullated fibres of the nerve centres are imbedded in an extremely delicate tenacious spongy connective substance, the peculiar consistence of which preserves the fibres from injury notwithstanding their softness, and the absence of any proper investing sheath.

The medullated fibres of the peripheric nerves, on the other hand, with the exception, perhaps, of those belonging to the optic and acoustic nerves, each possess in addition, and external to their medullary sheath, a special investment of connective tissue, constituting the so-called sheath of Schwann. This is either a structureless, perfectly transparent, delicate membrane, agreeing in its consistence and chemical constitution with the sarcolemna of muscular fibre, or consists of several layers of fibrillar connective tissue, and as in this presents nuclei scattered through its substance. If the membrane be very thin, the appearance of the medullated fibres is not materially altered by its presence. The refractive external border of the medullary sheath entirely prevents the extremely thin feebly refracting sheath of

Fig. 31.

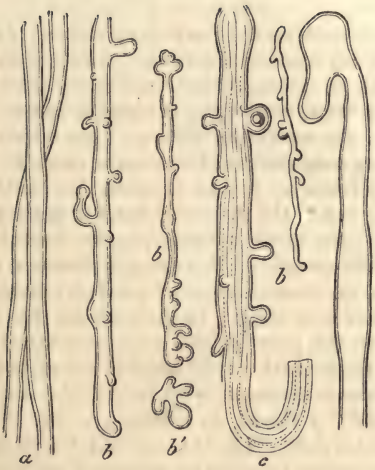

Fig. 32.

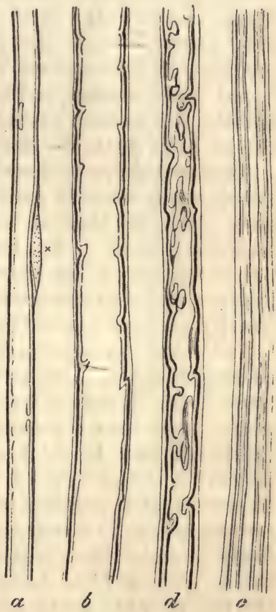

Fig. 31. Medullated nerve fibres destitute of the sheath of Schwann, recently removed from the fresh spinal cord. *a*, two unaltered fibres; *b b b*, fibres in which the medullary substance is swollen up by imbibition into irregular drops upon the surface; *b'*, a detached drop of the same nature (a so-called myelin drop); *c*, axis cylinder projecting from the medullary sheath.

Fig. 32. Medullated nerve fibre invested by Schwann's sheath, quite fresh. *a*, with a nucleus in the sheath at *x*; *b*, a very broad fibre; *c*, two very delicate and closely approximated fibres; *d*, a fibre so changed by manipulation that it exhibits the so-called coagulation contours.

From the lumbar plexus of a Frog.

Schwann from being seen. But the resistance and firmness of the several nerve fibres are extraordinarily augmented by it, and the facility with which long portions of the fibres may be isolated in the peripheric nerves depends essentially on its presence. It prevents also the occurrence of the

phenomena due to imbibition of fluids by the medullary portion of the nerves, as well as the formation of varicosities which are so characteristic of the medullated fibres of the nervous centres (fig. 31). The extraordinary differences in appearance and consistence exhibited by fibres of equal size, and similarly composed of axis cylinder and medullary sheath, but belonging respectively to the central and peripheric portions of the nervous system, are essentially referable to the presence or absence of this sheath of Schwann. In some instances the sheath is sufficiently thick to admit of measurement, as, for example, in the solitary nerve fibres that run in the mesentery of the frog, or in the electrical organs of the torpedo, where it attains a still greater thickness; * or it may even consist of a series of interlacing tubes, as in the nerves supplying the electrical organ of the electrical eel (Malapterurus), which are as thick as a knitting-needle, and still contain only a single medullated primitive nerve fibre.† In these instances the nuclei in the sheath are also much more distinct. If the sheath be very thin, it only becomes visible in the fresh state projecting for a short distance beyond the torn extremity of the fibres. Destruction and removal of the nerve medulla, in consequence of putrefaction or the action of reagents (concentrated acids, alcohol, and ether, which last dissolves the fat of the medullary sheath), are in such cases the only means by which the sheath of Schwann can be more distinctly demonstrated.

Just as a delicate sheath of Schwann, investing the medullary portion of the nerve, is scarcely perceptible in the fresh state of the nerve, so is it with great difficulty that an axis cylinder can be distinguished within the fresh medullary sheath. The bright lines which limit externally the highly refractive substance of the latter material, and the scroll-like contour lines which are occasioned by the gradually progressing coagulation of the nerve medulla, usually prevent the difference in the refractive power between the axis cylinder and the medulla from being observed. On the other hand it is easy to isolate the axis cylinder, at all events for short distances, in the medullated fibres of the central organs, when the sheath of Schwann is deficient; and it may thus be demonstrated from an examination of perfectly fresh specimens that in thick medullated fibres it is thick; in thin fibres, thin; appearing in the form of a pale fibre with the peculiarities above described. Moreover, it is possible in the perfectly fresh thick medullated fibres of the central organs to recognize distinctly the axis cylinder, with its fibrillar and finely granular structure, *within the medullary sheath*, as is shown in fig. 33, taken from a fibre from a brain of the torpedo. On this ground I regard the last possible doubt concerning the formerly frequently contested pre-existence of the axis cylinder as entirely set aside.

The isolation of the axis cylinder is remarkably facilitated by the previous application of fluids which gradually harden albuminous substances, such as dilute solutions of chromic acid, bichromate of potash, corrosive sublimate, and others. If these are allowed to act when in a moderate state of concentration, they harden the axis cylinder without any considerable troubling or granular coagulation, whilst the medullary sheath becomes crumbled and friable. In specimens of such medullated nerve fibres, as, for example, in those from the columns of the spinal cord, the axis cylinders may be either partially or completely isolated from the

* See Rud. Wagner, *Ueber d. fein. Bau des Elect. Organes im Zitterrochen*, 1847, fig. 3, *b*, and woodcut 35 in this work.

† Bilharz, *Das Elekt. Organ des Zitterwelses*, p. 21.

medullated sheath, for long tracts, with extreme ease; whilst the peripheric nerves, on account of the resistant sheath of Schwann, furnish preparations of less excellence. In order to see the axis cylinder *in situ*, fine transverse sections should be made through a carefully hardened spinal cord or nerve, and this should then be tinted in the ordinary method with carmine. The axis cylinder will now be found to be stained red, whilst the medullary sheath remains uncolored. The unavoidable shrinking of the soft watery axis cylinder, which occurs when the preparation has been kept in alcohol, causes transverse sections of the reddened axis cylinder to present for the most part a dentated contour line, and to occupy much less space than might be expected from examination made upon fresh nerve fibres. Moreover, in tinted preparations, the red axis cylinder may be seen to run longitudinally in the unstained medullary sheath, especially if this be rendered transparent by treatment with creosote or oil of turpentine. Transverse sections of the spinal cord are admirably adapted to exhibit the extraordinary variations that occur in the thickness of the axis cylinder, and the methods of Pflüger and Waldeyer are those which are best adapted to bring the axis cylinder speedily into view in fresh nerves. Pflüger's plan consists in adding a drop of collodion, Waldeyer's in adding a drop of chloroform, to the preparation, in as dry a state as possible, and covering with a thin glass. The medullary sheath will then be found to have lost its brilliancy, and in the greater number of nerve fibres the axis cylinder appears very distinctly as a finely granular central fibre.

Fig. 33.

Broad medullated nerve fibre, taken fresh from the brain of the Torpedo, in the interior of which the structure of the axis cylinder can be recognized.

We are in possession of extended observations by Bidder and Volkmann,* in reference to the difference in thickness existing amongst the peripheric medullated fibres, and especially between the cerebro-spinal and sympathetic fibres, which is very considerable.

A fourth form of nerve fibre may be added to those already described, which also occurs in the peripheric nerves, but is distinguished from the foregoing by the absence of the medullary sheath, and is on this account usually described as the peripheric non-medullated nerve fibre. These consist of fibres composed of a thicker or thinner bundle of primitive nerve fibrils, according to the kind of axis cylinder present, united together by a nucleated sheath of Schwann. All the branches of the olfactory nerve in the mucous membrane of the nose of all Vertebrates consist of such non-medullated nerve fibres. They are also of frequent occurrence in the sympathetic, the branches of which, distributed to the intestines, are often entirely composed of them; as, for example, the thick splenic nerves of Ruminants, which are often more than a millimetre in diameter. It was here that Remak first observed them,† and hence the non-medullated sympathetic fibres bear the name of Remak's fibres. Remak himself subsequently called them ganglionic fibres.‡ Some fibres show the fibrillar structure much

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* *Die Selbstständigkeit des Sympathischen Nervensystems.* Leipzig, 1842.

† *Observationes Anatomicæ et Microscopicæ de Systematis Nervosi Structura.* Berol., 1838.

‡ *Monatsberichte der Berliner Akademie*, 1853, 12th May.

more distinctly than others, as was remarked by Pflüger,* in the course of his investigations on the nerves of the salivary glands, on which account he divided them into two varieties. It is this kind of nerve fibre which, with few exceptions, is present amongst the Invertebrata. Nerve cords, which consist of such fibres, do not possess the bright glancing appearance of ordi-

Fig. 34.

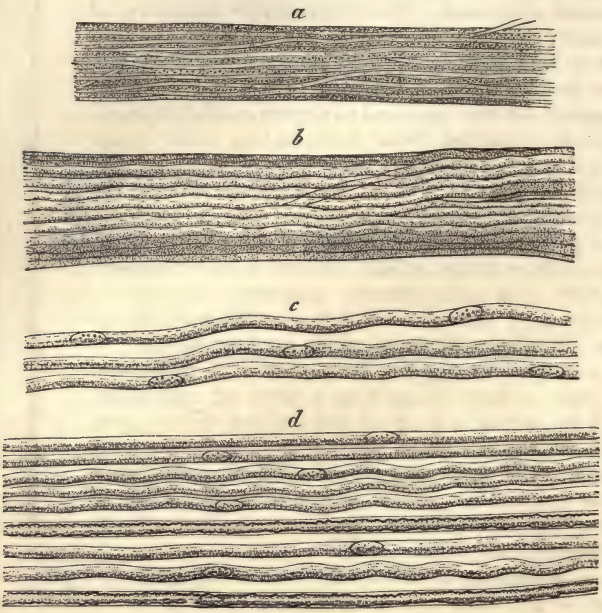

Fig. 34. Medullated nerve fibres. *a*, from the olfactory nerve of the Pike; *b*, from the olfactory nerve of Man; *c*, from the sympathetic (splenic nerve) of the Ox; *d*, from the nerve passing to the organ of Jacobson in the Sheep. In this specimen are two medullated fibres.

nary nerves, but are semi-transparent gray, gelatinous, and resemble embryonic tendinous tissue. If they are freed from the denser connective tissue which invests them, they can be broken up into their constituent fibres as easily as other nerves, which is a consequence of the firm consistence of the sheath of Schwann surrounding each fibre. The diameter of these non-medullated nerve fibres varies very considerably. In the sympathetic they scarcely exceed that of the medium-sized medullated fibres, but in the olfactory nerves of many animals fibres may be found at least three or four times thicker than the largest medullated fibres. Such thick fibres are shown in fig. 34, *a*, taken from the nasal fossa of a pike, consisting, when fresh, of a very soft, almost fluid, finely granular mass, with parallel striæ, contained in a transparent and structureless sharply defined sheath, in which, on the addition of acetic acid, nuclei made their appearance. By carefully hardening the specimen the fibrillar structure becomes very distinct, whilst at the same time the whole contents of the sheath may be

* *Die Endigungen der Absonderungsnerven in den Speicheldrüsen*, "On the Mode of Termination of the Secretory Nerves in the Salivary Glands." Bonn., 1866, p. 31.

broken up into fibrillæ of the nature of primitive nerve fibrils, between which the fine granules and molecules are interspersed to constitute an interfibrillar mass. In Man and most other vertebrate animals the fibres of the olfactory nerve are of less diameter than in fish, and resemble rather those of the sympathetic nerve, except that they are arranged in bundles within a common nucleated sheath, so that funiculi are formed similar to those shown in the subjoined fig. 34, *b*, taken from man. Here, as in the sympathetic nerve *c*, the substance of the individual fibres is fibrillar, and finely punctated, and probably consists of primitive fibrillæ and an interfibrillar substance.

According to the preceding account of the structure of the nerve fibres, the following kinds may be distinguished:—

1. Primitive fibrils.
2. Fasciculi of primitive fibrils.
3. Primitive fibrils with medullary sheath.
4. Fasciculi of primitive fibrils with medullary sheath.
5. Fasciculi of primitive fibrils, invested by the sheath of Schwann (as in the non-medullated nerve fibres of the sympathetic, the olfactory nerve, and the nerves of the greater number of invertebrate animals).
6. Fasciculi of primitive fibrils, with medullary sheath and the sheath of Schwann (as the fibres of most of the cerebro-spinal nerves).

1 and 2 may be distinguished as *naked* axis cylinders; and where they are invested by a sheath, as simply axis cylinders. It remains undecided whether nerve fibres exist, possessing a medullary sheath and the sheath of Schwann, the axis cylinder of which is formed by a single primitive nerve fibril.

If the nerve fibres be divided into two groups, according to the presence or absence of the medullary sheath, they may be further subdivided into

I. Non-medullated fibres.
   1. Primitive fibrils.
   2. Fasciculi of primitive fibrils.
   3. These last, with a sheath of Schwann.

II. Medullated fibres.
   1. Primitive fibrils with medullary sheath.
   2. Fasciculi of primitive fibrils with medullary sheath.
   3. These last with a sheath of Schwann.

We see then that the primitive fibril forms the elementary constituent of all nerve fibres. The variations that are observed are dependent on the number of the fibrils united together to form one cord, and upon the absence or presence of the medullary sheath and the sheath of Schwann. It is at once obvious how complicated a structure one of the so-called medullated primitive nerve fibres is when it is found to be composed of a bundle of primitive fibrils united by interfibrillar material constituting the axis cylinder, and of two investing sheaths.

The foregoing description differs from that generally received in the acceptance of the primitive fibrils, as the ultimate structural elements of the nerve fibres. I have already elsewhere * shown the probability of the existence of a fibrillar structure in the non-medullated fibres of the olfactory and sympathetic nerves, which the greater number of observers have regarded as purely granular rather than fibrous; and my views have been supported by later observers, as Waldeyer, † Pflüger, ‡ and others.

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* *Untersuchungen über den Bau der Nasenschleimhaut*, p. 63.

† *Zeitschrift für rationelle Medicin*, Band xx., 1863, p. 202.

‡ *Die Endigungen der Absonderungsnerven in den Speicheldrüsen*, 1866, p. 31.

We must here also take into consideration the similarity of the nerve fibres of the greater number of invertebrate animals, which all recent observers agree in describing as consisting of fasciculi of fibrils with interfibrillar granular substance.* Many Crustacea make exceptions to this, but only in so far that in them a structure analogous to the medullary sheath is present, in the interior of which fasciculi of fibrils lie enclosed, forming a kind of axis cylinder.†

Since their first discovery by Remak, the axis cylinders of the medullated nerve fibres of man and other vertebrates have repeatedly been held to exhibit a fibrillar structure. Remak himself described the axis cylinder, or as he termed it, believing it to be hollow, the axis tube, as marked by parallel lines, and regarded this as an indication of its fibrous nature.‡ His followers, however, became more and more convinced that the axis cylinder was a homogeneous structure, and this has recently been maintained by Waldeyer, to whom we are indebted for a laborious work on the subject.§ Waldeyer admits the probability of the origin of the axis cylinder from isolated fibrils in the nerve centres, just as he acknowledges that it splits peripherically into fibrils, but he holds that in its course it is a homogeneous structure.

Kölliker has arrived at the same result, since after adducing numerous arguments in favor of the fibrillar nature of the axis cylinder, he concludes with these words: "There is no absolute and decisive proof of fibrillation in the axis cylinder."‖

I am very far from denying that the axis cylinder, as it is ordinarily brought into view, gives the impression rather of a homogeneous than of a fibrillated cord. There is no doubt that when examined with moderate powers, and when hardened by the ordinary methods, its substance does appear homogeneous, or presents only a linear arrangement of fine molecules. But in proportion as the process of hardening is avoided in the prosecution of the investigation, and the structures are maintained, both as regards their consistence and refractive powers, in a state analogous to the fresh condition, especially when high magnifying powers are employed, so much the more clearly am I able to recognize a parallel striation and a substance of a finely granular nature between the striæ, which are appearances that I can only refer to the axis cylinder being constructed of fibrils, and an interfibrillar substance. For this investigation I especially employ the lateral columns of the spinal cord with their thick medullated fibres, from which, on account of the absence of the sheath of Schwann, it is easy to isolate the axis cylinder, not only when quite fresh, with the addition only of a little serum, but still better after twenty-four hours' or more maceration in solution of iodine in serum, in which the axis cylinder becomes slightly hardened without shrinking or otherwise materially altering in appearance. Perosmic acid is also here of great service, solutions of which, varying in strength from one-half to one-eighth per cent., acting for a short time on the axis cylinder, harden it without materially changing its volume, and without producing a trace of granular coagulation. Axis cylinders thus freed from the medullary sheath show with remarkable distinctness the characters of parallel striation. But even whilst still contained within the medullary sheath, the fibrous and granular structure of the axis cylinder may be observed, as I was first convinced from observations made on the thick fibres of the brain of the torpedo, which possesses a proportionately thin medullary sheath.¶

A decisive argument in favor of the fibrillar structure of the axis cylinder is derived from the observation of its origin from the great nerve cells of the spinal cord or of the brain. In regard to this point I must refer to the following account, and to the essay I have just cited, in which the particular observations are given, and will only mention here that the fibrils which emerge in a convergent direction from the cell substance, in order to form the axis cylinder process of the cells, unite, and are often far removed from one another by interfibrillar material (see figs. 29, 42, and 43, at *a*.) The formation of the proper axis cylinder results from a diminution in the quantity of the interfibrillar material, whilst the fibrils become more closely approximated in their parallel course, so that ultimately only a very small quantity of interfibrillar substance remains. In the periphery also it is not difficult to see the fibrillar character of solidary axis cylinders, as, for example, in the corpuscles of

* Cf. especially Leydig, *Lehrbuch der Histologie des Menschen und der Thiere*, 1857.

† Remak and Häckel, the last in Müller's *Archiv*, 1857, p. 469.

‡ *Observationes Anatomicæ*, etc., 1838, p. 2, note 2.

§ *Zeitschrift für rationelle Medicin*, Band xx., 1863, p. 193.

‖ *Gewebelehre*, fifth Aufl., 1867, p. 244.

¶ See my Essay, entitled *Observationes de cellularum, fibrarumque nervearum Structura*, *Bonner Universitäts-Programm*, 1868, fig. 5, and the preceding woodcut, 33, p. 121.

Vater and Pacini, as was shown to me by Dr. Grandry, providing the specimens are examined in the perfectly fresh state, without other addition than that of serum, and with sufficiently high powers.

I consider it, indeed, to be possible that, notwithstanding these observations, axis cylinders exist in which the original fibrillar nature is entirely lost by fusion of the fibrils with each other, and which have thus become homogeneous; but I regard the principle as correct, that the thicker axis cylinders are composed of several primitive fibrils, since these converge at the centric, and for the most part separate from one another at the peripheric extremity. On physiological grounds also I maintain the possibility of isolated conduction in these constituent fibrils, even when no trace of interfibrillar substance is present.

I may just add that my views on these points differ essentially from those of Stilling,* who indeed regards the axis cylinder as a complicated fibrous structure, but distributes his elementary fibrils generally on the surface, and considers that they unite with constituents of the nerve and medulla, which also again consists, according to him, of fine fibres or tubules. Stilling, as is well known, has not been able to distinguish the preformed structure from the products of coagulation that occur in nerve fibres hardened in chromic acid.

Both naked axis cylinders, and those enclosed in a medullary sheath, offer some remarkable and unexplained peculiarities when they are saturated with dilute solutions of nitrate of silver in the dark, and are then exposed to light. After Frommann,† who made the first observations on the point, the best subsequent investigations have been made by Dr. Grandry.‡ As a result of this treatment there occurs in the axis cylinder a fine transverse striation, caused by the partial deposition of brownish-black silver compounds, which is here and there so regular as to remind the observer of the structure of striated muscular tissue, though in other parts it exhibits great irregularity. When the action of light has been more protracted, the appearance in question gradually disappears, and the whole becomes equably tinted of a brownish black. As Grandry remarks, however, not only the axis cylinder, but also the branched processes of the ganglion cells, and frequently the cells themselves, exhibit this striation in a very surprising manner. No one has hitherto succeeded in showing any relation between these appearances and the finer structure of the parts.

1. Division of the Nerve Fibres.

A peculiar feature presented by the nerve fibres in their course is their division. This frequently occurs near their peripheric extremity, but is also to be observed in the nerve centres, and occasionally in the nerve trunks. It may take place in all kinds of nerve fibres, with the exception of the primitive fibrils. Branched and ramified fasciculi of primitive fibrils are composed of the processes of many multipolar ganglion cells. In the olfactory nerve may be seen the repeated subdivisions, quickly following each other, of non-medullated fibres provided with a sheath of Schwann, with the sheath prolonged upon the branches.§ The mode of division, however, that has been most frequently described is that of the medullated fibres, such as is seen, for example, in the nerves distributed to muscle.‖ This mode of division is usually dichotomous, and affects all the constituents of the nerve fibre. The division of the fibrillar axis cylinder probably consists only in a gradual process of isolation of the associated primitive fibrils. The medullary sheath is continued at the point of division over the

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* *Neue Untersuchungen über den Bau des Rückenmarkes*, 1859, p. 708.

† Virchow's *Archiv*, Band xxxi., Taf. 6, figs. 11 to 16.

‡ *Recherches sur la Structure intime du cylindre de l'axe et des cellules nerveuses*, *Bulletin de l'Académie Royale du Belgique*, *Mars*, 1868.

§ This may be particularly well observed in the thin plates of the nasal fossæ of rays and of sharks. Max Schultze, *Bau der Nasenschleimhaut*, Taf. 4, fig. 8, v. 9.

‖ See in particular Reichert and Müller's *Archiv*, 1851, p. 29. E. Brücke and Joh. Müller were the first who observed the divisions of medullated nerve fibres in muscle. See the last-mentioned author's *Handbuch der Physiologie*, fourth edition, Band i., p. 524. Paul Savi was the first who saw the primary divisions of medullated nerve fibres in the electric organs of the Torpedo, in 1844.

branches, and is finally lost at their extremities. It is very remarkable that at the point of division, in consequence of a sudden diminution in the quantity of the nerve medulla, an attenuation of the nerve fibre occurs, whilst beyond this point, when the division is completed, the medulla is again found in its ordinary proportion. The sheath of Schwann divides in pre-

Fig. 35.

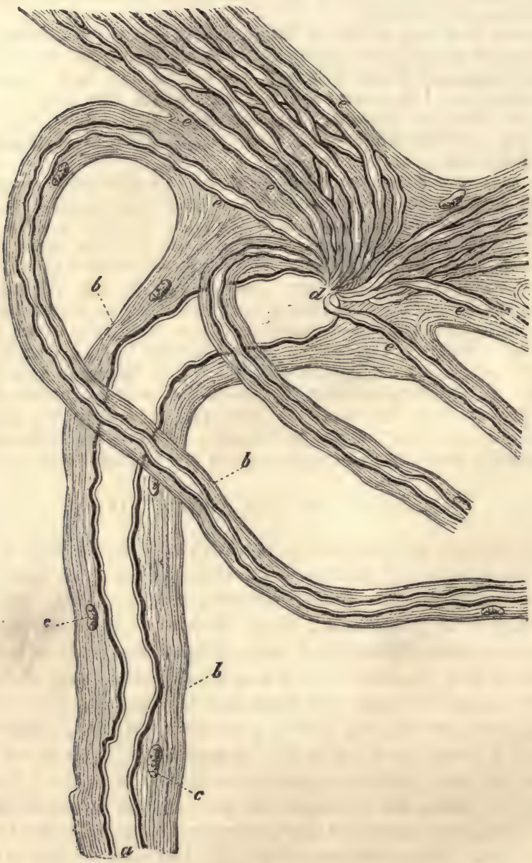

Fig. 35. Medullated nerve fibre, from the electric organ of the Torpedo, at the point of division, presenting a very thick sheath of Schwann. *a*, trunk fibre; *b*, sheath; *c*, nucleus of the sheath; *d*, point of division; *e*, branches. After R. Wagner.

cisely the same manner. As the branches after division are much thicker when taken collectively than the trunk from which they proceed, whilst the axis cylinders diminish, it is obvious that the sheaths must augment in thickness. This holds in particular for the medullary sheath, the thickness of which is proportionately much greater when the axis cylinder is thin than when it is thick. Instead of the dichotomous division, three, four, or more, even up to five-and-twenty branches may suddenly arise from a single trunk

fibre, as was first observed by Rud. Wagner in the nerves of the electric organ of the Torpedo.* By far the most remarkable example of nerve division occurs, however, in the electric eel (Malapterurus electricus). Here, according to Bilharz, each of the two electric organs which lie like masses of bacon-fat beneath the skin, receives a nerve from the medulla oblongata, consisting of only a single medullated fibre, having a diameter of 0·025 millimetres,† which, in order that it may give a peripheric terminal fibre to each electrical plate, must divide millions of times.

The sheath of Schwann disappears sooner or later in the process of division, and is consequently absent in the ultimate fibrils, as may be seen, for example, in the nerves of the cornea. Here the medulla also sooner or later disappears from the surface of the axis cylinder. Coincidently, or somewhat later, the sheath of Schwann can no longer be distinguished, the axis cylinder, which alone remains, repeatedly divides, and the fine primitive fibrillæ, as first demonstrated by Hoyer ‡ and Cohnheim,§ ultimately project from the sub-epithelial tissue between the cells of the tesselated epithelial layer of the conjunctiva corneæ, and terminate by free extremities at the surface. The same appearance may be seen in many other nerves, as in the acoustic and optic, in the nerves of the tongue, in those distributed to the glands and elsewhere, though in these instances each primitive fibril is connected with a peculiar terminal apparatus, which will be hereafter described. In many parts, however, the division into primitive fibrils does not take place; that is to say, an axis cylinder of appreciable diameter terminates, so far as we at present know, without previously breaking up into the finest nerve filaments. The above-mentioned examples, the nerves distributed to many electrical organs, to the transversely striated muscles, the Vater's (Pacini's) corpuscles, exhibit, in part at least, when carefully examined, no exception to this rule.

2. Of the Peripheric Terminal Organs.

The peripheric division into primitive fibrils appears to occur in all the nerves of special sense, but especially in those cases where perception of a great variety of impressions occurs within a very limited space. Peculiar terminal organs are found in such instances in connection with each fibre, of which a more detailed description will be given in the consideration of the different senses, but which will be here only regarded from a general point of view. In the nasal mucous membrane, fusiform easily alterable cells are found occupying interspaces between the palisade-like cells of the olfactory region. These possess a centric and a peripheric process, of which the former exactly resembles the primitive nerve fibrils of the olfactory nerves,‖ whilst the latter either ends at the level of the free surface of the epithelial cells, as in man, mammals, and fishes, or extends beyond this sur-

* *Feiner Bau des Elekt. Organes im Zitterrochen*, "Minute Anatomy of the Electric Organs of the Torpedo," 1847, p. 17.

† According to Bilharz, *loc. cit.*, p. 22—$^{1}90^{iii}$.

‡ *Ueber die Endigungen der sensibeln Nerven in der Hornhaut*, Virchow's *Archiv*, Band xxxviii., 1867, p. 343.

§ Reichert and Du Bois Reymonds' *Archiv*, 1866, p. 180.

‖ The existence of these cells was first recognized by Eckhard in the frog. See his *Beiträge zur Anatomie u. Physiologie*, Band i., 1855, p. 17, Taf. 5, figs. 3, 4 *c*; and a discussion on their relation to the Nervous System will be found in Schultze's Essay in the *Monatsberichte der Berliner Akademie*, 1856, November, p. 504, and at still greater length in Max Schultze's *Untersuchungen über den Bau der Nasenschleimhaut*, Halle, 1862, with five plates.

face in the form of a long stiff hair, or of several finer hairs, analogous to cilia, but incapable of movement.

I have named these cells *olfactory cells*, and the hairs *olfactory hairs*. The general relations are the same in the mucous membrane of the tongue, as Axel Key * has shown in the papillæ fungiformes of the frog, and Schwalbe † and Loven ‡ in the gustatory cells of the papillæ circumvallatæ, and of some of the fungiformes in man and mammals. These terminal organs corresponding to the olfactory cells may be termed *gustatory cells*. Similar conditions are found in the auditory organs, since in those parts where the nerve terminations are simple, the terminal branches of the medullated acoustic fibres, after losing their medullary sheath, penetrate between the epithelial cells, especially between those of the otolith sacs and of the ampullæ of the semi-circular canals, and after breaking up into primitive fibrils become continuous with peculiar ciliated auditory cells.§ The mode of termination of the nerves in the cochlea is of greater complexity, especially because a portion of the non-nervous cells of the epithelial investment of the cochlear canal develops into the several structures forming the organ of Corti. But even here the terminal nerve structures appear to consist of cells supporting hairs, which are continuous with extraordinary delicate non-medullated nerve filaments (primitive fibrils). The terminal nerve apparatus of the optic nerve in the retina presents quite peculiar features. Here are found the *layer of rods and cones*, and the nucleated external granules, which last, like the terminal apparatus of the olfactory nerve, appear as fusiform cells, with a centric and a peripheric process. The centric process of the rods is a single primitive fibril, but that of the cones is a fasciculus of primitive fibrils.‖ The peripheric process terminates in the case of the so-called rods and cones in an essentially similar manner, the extremity in each consisting of a pale inner segment resembling ganglionic cell substance, and a bright highly refractile external segment, which is separated from the former by a sharply defined line, and which in the rods is of cylindrical, and in the cones of conical form. The structure of the outer segments, which, in all probability, constitute the proper terminal structures, upon the excitation of which perception depends, differs from that of any other nervous organ, especially in its consisting of a series of thin plates superimposed on one another in the direction of its long axis.¶ The tactile nerves of the skin, lastly, terminate in the so-called *tactile corpuscles*, which are oval or spherical, very soft, and easily alterable bodies,

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* Müller's *Archiv*, 1861, p. 329.

† *Archiv für Mikroskop. Anatomie*, Band iii., p. 154; Band iv., p. 154.

‡ *Idem*, Band iv., p. 96.

§ See Max Schultze's *Ueber die Endigungsweise des Hörnerven im Labyrinth*, Müller's *Archiv*, 1858, p. 343; Franz Eilh. Schulze in *idem*, 1862, p. 381; Odenius, *Archiv für Mikroskopische Anatomie*, Band iii., p. 115. Hasse so far gives a different account, in that he has not been able to observe the division of the axis cylinder into finer filaments (primitive fibrils). See others in *Zeits. für wissens. Zool.*, Bd. xvii., p. 638; Bd. xviii., p. 89. I must, however, maintain the correctness of my assertions respecting and illustrations of the above-described objects. The consideration of the auditory organ of invertebrate animals is of great importance in regard to the relations in question. See Hensen, *Zeitschrift für wissenschaftliche Zoologie*, Band xiii., p. 319, "On the Auditory Organs of the Crab."

‖ Max Schultze, *Archiv für Mikroskopische Anatomie*, Band ii., Taf. 10.

¶ Max Schultze, *Archiv für Mikroskopische Anatomie*, Band iii., p. 215. A reference may also be made to the differentiation of one or several axial fibres in the outer segment, first observed by Ritter. See especially Hensen, Virchow's *Archiv*, Band xxxix., p. 475, Taf. 12.

occupying the interior of many tactile papillæ of the skin,* each of which is continuous with one or more medullated nerve fibres that divide in their interior, though up to the present time the precise mode of termination of the primitive fibrils in them has not been completely elucidated.

In immediate relation to the sense of touch stand also in all probability the nerve hairs found on the surface of young fish and naked amphibia, which have been described by F. E. Schulze,† and the arrangement of which in the form of pencils or brushes calls to mind the nerve hairs in the ampullæ of the auditory organ. These appear to be well adapted for the perception of movements of the water in which the animals live. In fishes also is found the lateral canal system, with the nerve bulbs described by Leydig. I have also observed a very similar disposition of the nerves in regard to hair-bearing epithelial cells in the vesicles of Savi present in the torpedo.‡ According to recent investigations by Franz Boll, the highly nervous ampullæ of the so-called mucous canals of the head of rays and sharks are covered with cell-supporting hairs.

We may also regard the *corpuscles of Vater or Pacini* as constituting terminal organs of the sensory nerves. These are most commonly found in man in the subcutaneous connective tissue of the sides of the fingers and toes, seated on the volar and plantar nerves; also on the nerves supplying joints, and in the nerves coursing between various muscles of the trunk and extremities;§ in animals, however, they are found in many other parts of the body, and may be most easily obtained for examination from the mesentery of the cat. Each of these corpuscles receives a medullated nerve fibre, which does not again emerge from it. The corpuscle itself consists of many concentrically arranged layers of connective tissue, becoming always more closely packed near the centre, and surrounding a cavity filled with soft abundantly nucleated and very easily alterable material, which undergoes coagulation after death, and into the interior of which the nerve fibres penetrate. These, after they have lost the medullary sheath and the sheath of Schwann, which becomes continuous with the laminated sheaths of connective tissue investing the corpuscle, consist only of the axis cylinder, which terminates in a little bulb.‖ Dr. Grandry, who has examined the Pacinian corpuscles with higher magnifying powers than appear to have been previously employed, observed a very distinct fibrous structure in the axis cylinder in their interior, and also that the terminal bulbs consist of finely granular substance, from which the diverging terminal fibrils may be clearly distinguished. Closely allied to the foregoing are the numerous terminal nerve corpuscles described and depicted by Krause as existing in the conjunctiva, the genitals, and other parts of the body, which differ from the Pacinian corpuscles only in the absence of a thick laminated investment.¶ The mode of ter-

* We owe the discovery of these structures to Meissner and Rud. Wagner. See Göttinger *Nachrichten*, 1852, No. 2; or in more detail Meissner, *Beiträge zur Anatomie und Physiologie der Haut*. Leipzig, 1853.

† Müller's *Archiv*, 1861, p. 759.

‡ *Untersuchungen über den Bau der Nasenschleimhaut*, 1862, p. 11. In this essay will be found a more detailed account of the relations at present known to exist between nerves and epithelial investments.

§ See Rauber, *Untersuchungen über das Vorkommen und die Bedeutung der Vater-schen Körper*, "Researches on the Distribution and Function of the Corpuscles of Vater," 1867.

‖ See the numerous illustrations of these corpuscles and their minute microscopic anatomy in Henle and Kölliker's Essay, *Ueber die Pacini'schen Körper an den Nerven des Menschen und der Säugethiere*, Zurich, 1844, which was followed by the work of Herbst, entitled *Die Pacini'schen Körper und ihre Bedeutung*, Göttingen, 1848. There are numerous recent investigations on the point, amongst others, those of Leydig, Krause, Kölliker, and Rauber.

¶ See W. Krause, *Die terminalen Körperchen*, 1860; *Anatomische Untersuchungen.*

mination of the nerves in the transversely striated muscles has been the subject of numerous researches, and we now know through those of Kühne, Engelmann, and others that axis cylinders of moderate thickness penetrate the sarcolemma of the muscular fibres, and either branch out to form the so-called terminal nerve plate, or, as in the frog, break up into primitive fibrils in the

Fig. 36.

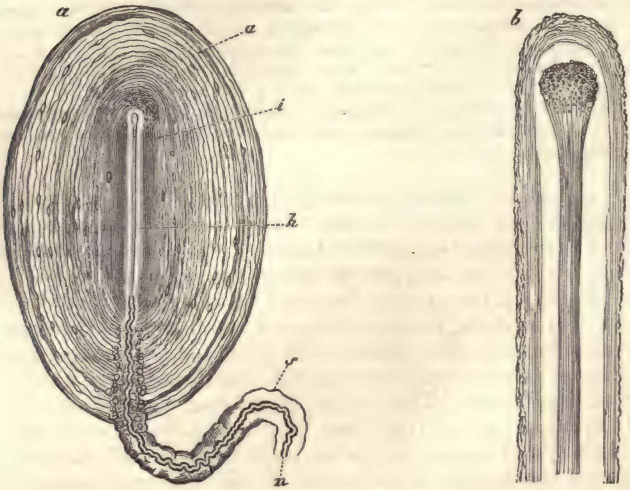

Fig. 36. *a*, Vater-Pacinian corpuscle from the mesentery of the cat, examined with a low power—after E. Ecker; *b*, the end of the nerve fibre, consisting of a fibrillated axis cylinder, the fibrils of which are lost in a finely granular mass, magnified 1,000 linear—after Grandry.

interior of the contractile substance, and therefore probably in the interfibrillar substance. Frankenhäusen has recently maintained that in the smooth muscular fibres there is a connection between the primitive nerve fibrils and the nucleoli of the fibre cells, on which point, however, the reader is referred, as in regard to the nerves of muscles generally, to the section on muscles.

A peculiar and remarkable mode of nerve termination is found in the electrical organs of those fish that are provided either with true or the so-called pseudo-electric organs (as the Torpedo, Malapterurus, and Gymnotus amongst the former, and the Raja and Mormyrus amongst the latter). The axis cylinders of the nerve fibres, which pass to these organs from the nerve centres, here terminate in the so-called electrical plates, which are direct expansions of the nerve fibres in the form of remarkable discs, each of which lies in a small chamber of the organ formed by septa of connective tissue. Fig. 37, after Ecker, taken from the Mormyrus, shows the electrical plates forming direct expansions of the nerve-fibre substance, from which it appears that the nerve fibres penetrate foramina in the plates (as in some species of Mormyrus and Malapterurus) before they break up in its substance.

The point of entrance always occurs on one only of the two surfaces of

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1861; Bense, *Die Nervenendigungen in den Geschlechts-Organen, in der Zeitschrift für rationelle Medicin*, 1868, Band xxxiii., p. 1.

the disk, and, indeed, on the same or corresponding surface of all the plates of the same animal; thus, for example, in the torpedo, in which the plates have a dorsal and ventral surface, the nerves are always applied to the ventral surface, the dorsal remaining smooth; consequently all these electric plates have a smooth free, and a rough surface to which the nerve fibres are attached, and these all look in the same direction. At the moment of the discharge in all the electric fishes hitherto examined, that side of the animal to which the rough surfaces of the electrical plates are turned is negative as compared with the opposite. In Malapterurus only a single primitive nerve fibre, which has just previously lost its medullary sheath, penetrates each plate; but in all other animals many fibres enter. The structure of these electric plates, composed of albuminous material, differs in two points from the former. The plates of the true electric organs are homogeneous disks,

Fig. 37.

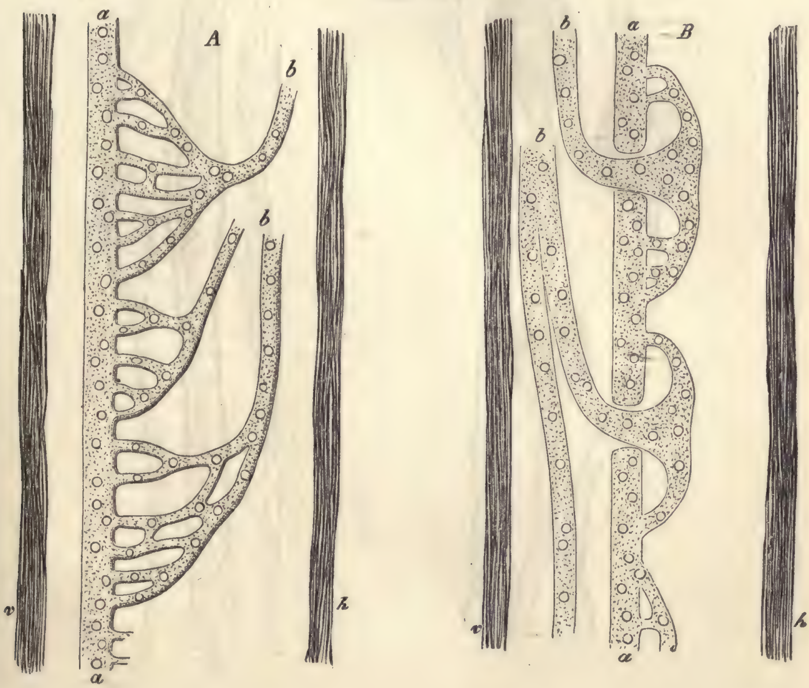

Fig. 37. *A*. From the electric organ of Mormyrus oxyrhyncus, and also as in the M. longipinnis and cyprinoides. *v* anterior, *h* posterior connecting tissue septum; *a a*, electric plates; *b b*, nerves penetrating into their interior.

B. From the electric organ of Mormyrus dorsalis, and also as in the M. anguilloides. Lettering as in *A*.

slightly uneven on their free surface, in the interior of which oval or spherical nuclei, surrounded here and there with a little finely granular substance, lie scattered at definite distances. The plates of the so-called pseudo-electric organs, on the other hand, exhibit similar nuclei, but their substance is not homogeneous, being marked by delicate, meandering, and looped systems of lines, which result from their complicated structure, composed of a number

of layers of very thin curved plates. The tissue in some measure calls to mind that of the transversely striated muscles.*

In regard to the mode of termination of the nerves in glands, the investigations of Pflüger † on the salivary glands may here be mentioned, in which

Fig. 38.

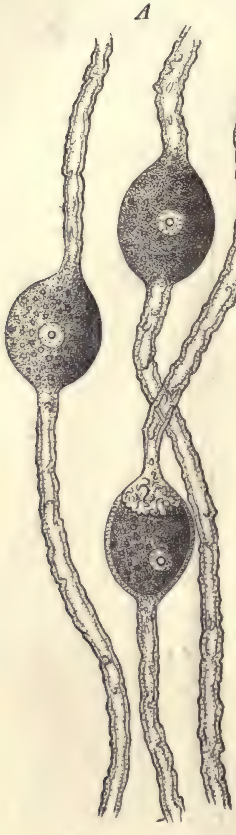

Fig. 39.

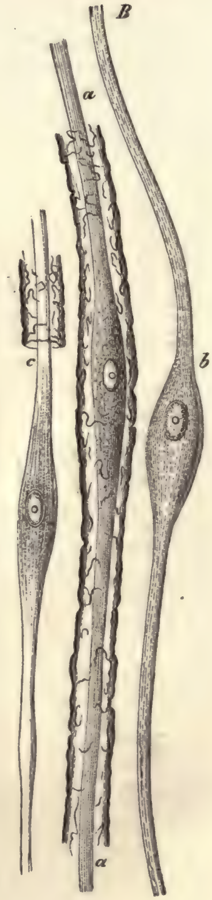

Fig 38. Three bipolar ganglion cells, from the Ganglion Gasserii of the Pike—after Bidder.

Fig. 39. Three bipolar ganglion cells, from the auditory nerve of the Pike. *a*, still contained in the medullary sheath; *b*, entirely; *c*, partially exposed, in order to show that these ganglion cells are only nucleated dilatations of the axis cylinder.

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* A. Ecker, *Untersuchungen zur Ichthyologie*, Freiburg, 1857; *Berichte der Naturf. Gesellschaft zu Freiburg*, 1858, No. 28. Max Schultze, *Ueber das Pseudo-elektrische Organ: Sitzungsberichte der Naturf. Gesellschaft in Halle*, 1857, p. 17; and in Müller's *Archiv*, 1858, p. 193. Also Bilharz, *Das Elektrische Organ des Zitterwelses*, 1857; and Max Schultze, *Zur Kenntniss des Elektrischen Organs der Fische*, 2 Abtheilungen. Halle, 1858 and 1859.

† *Die Endigungen der Absonderungsnerven in die Speicheldrüsen.* Bonn, 1866.

he showed that the extremities of the nerves formed such a connection with gland cells, that either the cells themselves or their nuclei constituted the terminal organ, as will be more explicitly described in the article on GLANDS.

Hensen has described the cutaneous nerves of the frog as terminating peripherically in the nucleoli of the cells of the epidermis.* They form extraordinarily fine fibres, which penetrate both the cells and nuclei, and in consequence of the frequent division of the nuclei are also themselves frequently bifurcated.

3. ON THE MODE OF ORIGIN OF THE NERVE FIBRES IN THE NERVE CENTRES.

The transition from the foregoing to the consideration of the central source or origin of the nerve fibres is to be found in the description of those nerve or ganglion cells which are intercalated in the course of the nerve fibres, and of the so-called ganglia. The microscopic examination of the ganglia of the brain and spinal cord, as well as of the sympathetic nerves, alike shows that the cells are to be regarded as an essential part of these structures, and that they exhibit a nucleus and nucleoli lying in a relatively considerable quantity of a dense finely-granular and fibrillated cell substance, which is often tinged of a yellow color. The greater number of these cells, when isolated in the perfectly fresh state in serum, are spheroidal; yet they are often also very irregular in outline, destitute of any doubly contoured investing membrane, and become broken up and disappear with the greatest facility. In sections made through fresh or hardened ganglia such cells appear to be arranged in layers surrounded by fibrous connective tissue, in which large numbers of both medullated and non-medullated nerve fibres commonly lie imbedded. Each cell, however, occupies a kind of capsule composed of nucleated connective tissue, from the inner surface of which it retracts when acted upon by strongly hardening fluids.

The majority, perhaps it may even be said all, of these cells possess processes, which, however, in the fresh state can be torn off with a facility proportionate to the difference in the consistence of the cell substance and the investing capsule of connective tissue. These processes are nerve fibres, as was first observed by Remak in the Vertebrata,† and by Helmholtz ‡ amongst the Invertebrata. If only one be present, causing the cell to look like a berry attached to its stalk, it is termed unipolar; if there are two which are often connected with the opposite extremities of the cell, this is termed bipolar, and when there are several, it is multipolar. That these processes are nerve fibres is most clearly evident in bipolar ganglion cells, which are introduced in the course of those medullated nerve fibres that may easily be obtained from the perfectly fresh spinal ganglia of sharks and rays, where they were first noticed by Robin and Rudolph Wagner § in 1847; or from the Gasserian ganglion of the same animals, where I have been able to demonstrate their presence with great ease; or from the same ganglion of the osseous fishes (pike, according to Bidder); ‖ or lastly, from the auditory nerve before its entrance into the sacculi of the labyrinth.¶ The

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* Virchow's *Archiv*, Band xxxi., p. 63, Taf. 2, fig. 14; *Archiv für Mikroskopische Anatomie*, Band iv., p. 121.

† Froriep's *Notizen*, 1837, Nos. 47, 56, 58; *Observationes Anat. et Microscop. de Systematis Nervosi Structura.* Berol, 1838.

‡ *De fabrica Systematis Nervosi Evertebratorum*, *Diss. inaug.*, 1842.

§ R. Wagner, *Neurologische Untersuchungen*, p. 7.

‖ *Zur Lehre von dem Verhältniss der Ganglionkörper zu den Nervenfasern*, "On the relations of the Ganglia to the Nerve Fibres." Leipzig, 1847.

¶ Max Schultze, *De Retinæ structura penitiori.* Bonn, 1859, fig. 7.

cell substance is here a continuation of the substance of the axis cylinder; it includes a nucleus and nucleoli; the medullary sheath usually ceases at the point of transition of the fibre into the nucleated enlargement of the axis cylinder, and reappears at the corresponding point on the opposite side; though it occasionally invests the entire cell, the cytoid enlargement of the axis cylinder in that case occasioning no interruption to the medullary sheath. It is obvious that such a ganglion cell is only a nucleated swelling of the axis cylinder. The fibrillated structure of the latter may be followed in the cell substance, although it is there in part concealed by the presence of a considerable quantity of the interfibrillar substance. And just as the medullary sheath is not essential to our conception of a nerve fibre, so we can only regard it as forming an accessory sheath to the ganglion cell, to which, indeed, it rarely constitutes a continuous investment. The sheath of Schwann, if present, is continued over the ganglion cell, and forms the above-mentioned capsule of nucleated connective tissue. It is, however, absent in the bipolar ganglion cells of the auditory nerve.

The structure of the spinal ganglia of other vertebrata and of man is more complex. It has been frequently observed, and has very recently been corroborated by the researches of Schwalbe,* that the cells of these ganglia each possesses for the most part only a single non-medullated process which runs towards the periphery, and which, according to Kölliker, subsequently becomes the axis cylinder of a medullated nerve fibre. Like the substance of the ganglion cells, it presents a fibrillated structure. From some of the cells, on the other hand, instead of a single process, several are given off, which, however, do not arise, as in fishes, from the opposite poles of the cells, and with the further course of which we are still unacquainted. Observations similar to these were made by Kölliker on the cells of the Gasserian ganglion.†

Like those of the spinal ganglia, the cells of the sympathetic ganglia are invested by dense connective tissue, and each possesses a proper nucleated capsule, proceeding from and continuous with the sheath of Schwann, covering the nerve fibres with which it is in connection. The number of these last here also varies to a considerable extent. In the sympathetic of the frog, which has been most frequently examined, there occur, besides such unipolar cells as have just been described, others from which two processes spring in close proximity, of which one winds spirally round the other. The minuter details respecting the mode of connection of these spiral fibres, which were first described by L. Beale ‡ with the ganglion cells, is still a subject of dispute, as is evident from the conflicting statements of J. Arnold,§ Courvoisier,‖ Kölliker,¶ and others. The existence of multipolar cells in the large ganglia of the sympathetic, though contested by many, is certain, as I have myself found such cells both in children and in adults (fig. 40). Unfortunately, on account of the surrounding fibrous connective tissue, it is impossible to isolate the processes for any considerable portion of their length.

The processes in connection with the ganglion cells of the spinal cord which furnish axis cylinders to the spinal nerves, those in the anterior horns of the gray matter proceeding to the motor, and those in the posterior

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* *Archiv für Mikroskopische Anatomie*, Band iv., p. 45.
† *Handbuch der Gewebelehre*, 5. Auflage, p. 319.
‡ *Philosophical Transactions*, 1863, Vol. cliii., p. 539.
§ Virchow's *Archiv*, Bände xxviii. and xxxii.
‖ *Archiv für Mikroskopische Anatomie*, Band ii., p. 13, and Band iii.
¶ *Handbuch der Gewebelehre*, 5. Auflage, p. 254.

horns to the sensory nerves, are much more accurately known. The researches of Deiters in particular have demonstrated that from every ganglion cell, however numerous its processes may be, only one peripherically coursing axis cylinder arises. This runs without branching, obtains, sooner or later, a medullary sheath, and passes into one of the roots of the nerves. It possesses a fibrillar structure, as I have myself most distinctly seen, both in sensory and motor and ganglion cells. The other processes of these ganglion

Fig. 40.

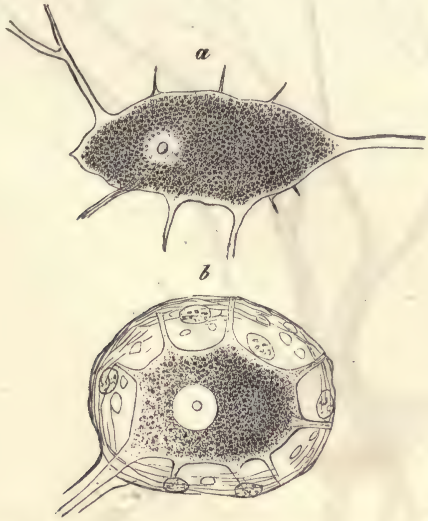

Fig. 40. Nerve cells from a lumbar sympathetic ganglion of an adult man. *a*, without a sheath; *b*, with a sheath. The cell substance contains pigment of a vivid yellow tint, and is consequently darkly granular.

cells, the number of which is greater in the large cells of the anterior horns than in those of the posterior, branch in an arborescent manner very soon after their origin. Their structure is also distinctly fibrillar; but the quantity of interfibrillar granular substance they contain is greater than in the axis cylinder process. The fine filaments (primitive fibrils), which result from their ramification, soon evade observation, and their ultimate destination is unknown. Deiters believes that in some few instances he has observed them to become invested with a delicate medullary sheath.

The fibrils of both kinds of processes arise from the ganglion cell substance itself, which exhibits a fibrillar structure throughout, though a finely granular substance, often containing yellowish or yellowish-brown pigment, also exists between the fibrils; this may extend into the branched processes, or after being interrupted for a greater or less extent, may again make its appearance in them. The fibrillar structure may be most distinctly perceived in the cortical portion of the ganglion cells, though it unquestionably extends into the interior. In many cases, and especially in young rather than in more fully developed ganglion cells, a considerable quantity of finely granular material appears to occupy the interior of the cell, and to surround the nucleus. The course of the fibrils within the ganglion cells is very complicated; they may be seen passing from the processes into the cell substance in a divergent manner in every direction, and are there lost

Fig. 41.

Fig. 41. Multipolar ganglion cell, from the anterior horn of the gray substance of the spinal cord of the Ox—after Deiters. *a*, axis cylinder process; *b*, branched processes. Magnified 300 diameters.

in the confused whorl of decussating filaments. This structure exists in the perfectly fresh state, as may be seen in the large cells of the fresh spinal cord which have been isolated after the addition of serum, and is very distinct in preparations macerated in perosmic acid and other hardening agents, which either check the natural conversion of the fibrils after death into a granular mass, or which do not produce any granular coagulation.

Remak* first called attention to this fibrillar structure, and it was subsequently further investigated in the ganglion cells of various parts by Leydig, Beale, Frommann, Arnold, Kölliker, and myself,† although up to the present time there has not been complete agreement between the different observers in regard to its nature.

In consideration of the great difficulty experienced in isolating fresh ganglion cells, and in determining their distribution, it appeared to me worth while to subject to severe scrutiny, in the fresh state, those parts of the brain of the Torpedo in which, as has long been known, large ganglion cells, similar to the motor cells of the spinal cord, are accumulated in great numbers.‡

It was most convincingly shown here that the large cells removed from the living animal, and prepared in serum, in which they were capable of being easily isolated, possess, both in their processes and in their proper substance, an exquisitely delicate fibrillar structure. In large specimens the interfibrillar substance is strongly tinged of a yellow color, and is in some parts coarsely granular. These circumstances render the investigation of the direction of the fibres difficult, so that young specimens are to be preferred for examination. Each of the numerous processes of these ganglion cells receives a compound fibril from the cell substance, giving the impression that the whole mass of fibrils given off by ganglion cells only traverse it. The nucleus of these cells is seen with a sharply defined outline lying imbedded in the finely granular fibrillated material, but does not appear to stand in any direct connection with the fibrils which cover its external surface. Its substance is homogeneous, and it contains in its interior a large nucleolus which stands out in strong relief as a highly refractive spherical body, and conceals one or more, rarely several vacuolæ. We may regard such a ganglion cell, from which a peripherically directed nerve fibre proceeds, as representing the source and origin of this axis cylinder, but only in the sense that the fibrils which compose the axis cylinder are collected into a group from the arborescent processes of the cell; and thus the fibrils which are seen traversing the substance of the ganglion cell do not originate in the cell, but only undergo a kind of arrangement in it, and then pass to the axis-cylinder process, or extend into the other branched processes.

The researches of Deiters have rendered it probable that at the origins of the cerebral nerves the groups of ganglion cells which were described by Stilling under the term nerve nuclei, contain ganglion cells which closely resemble those of the anterior and posterior cornua of the spinal cord, especially in the circumstance that they give off only one peripherically directed axis-cylinder process, the remaining processes breaking up into a ramification of primitive fibrils.

It is well known that a considerable number of ganglion cells are found

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* *Monatsberichte der Akademie der Wissenschaften zu Berlin*, 1853.

† See Kölliker, *Handbuch der Gewebelehre*, 5. Auflage, p. 251, and the woodcut on p. 275.

‡ *Observationes de Structura cellularum fibrarumque nervearum. Bonner Universitäts-Programm*, Aug., 1868.

F g. 42.

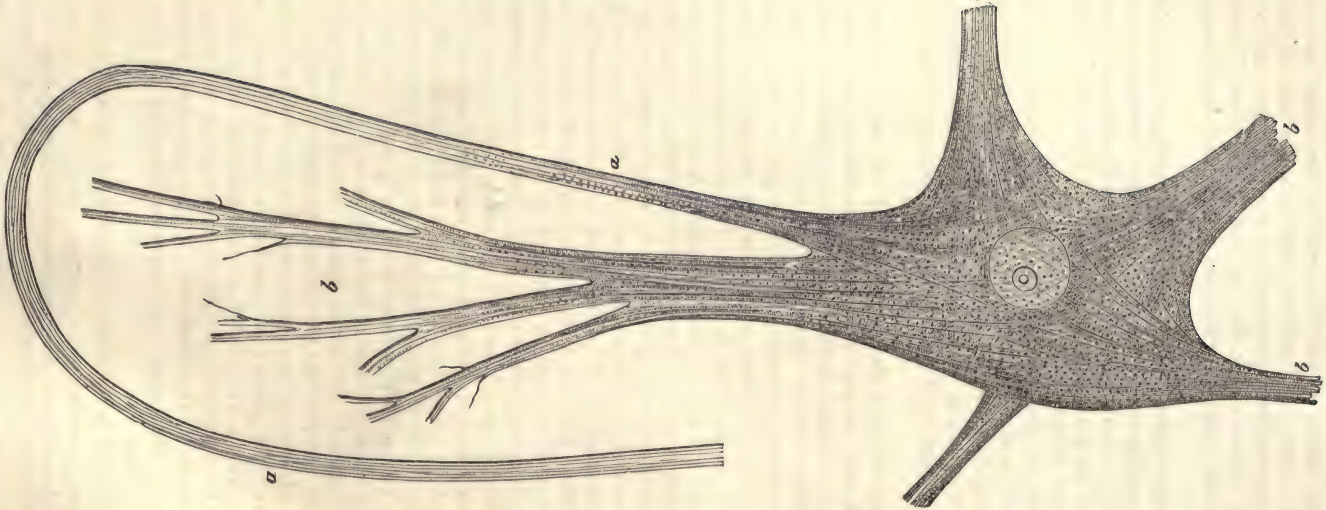

Fig. 42. A medium-sized ganglion cell from the anterior horn of the spinal cord of a Calf, isolated after short maceration in serum containing a little iodine in solution, x 600. Some of the processes are abruptly broken off, as may be seen in the three lower ones marked *b*; *a* is the axis-cylinder process.

distributed through the brain, which do not directly give origin to peripherically coursing fibres; as, for example, the retort-shaped ganglion cells of the cortex of the cerebellum, and the peculiarly shaped cells of the gray cortical layer of the cerebrum, for the exact description of which we are indebted to the recent investigations of Rudolph Arndt* and Meynert.† In the former, according to Deiters,‡ the azygous process directed towards the white substance of the cerebellum corresponds to the axis-cylinder process; and it is known that the peripherically coursing processes of these cells branch in an aborescent manner. Other microscopists, as Gerlach,§ have observed ramifications occur in the centrically directed process. It is therefore scarcely justifiable, in the present state of our knowledge, to institute a precise comparison between these cells and those which are found in the spinal cord. On the other hand, I have myself seen a fibrillar structure in these ganglion cells of the cerebellum and their peripheric processes with the utmost distinctness, as, indeed, had previously been observed by Kölliker in their processes,‖ so that in this respect there does not appear to be any difference between the two sets of cells. The same holds good for the cells of the gray cortex of the cerebrum. As Meynert and Arndt state, these possess a thicker peripheric process and a large number of branched processes, which are directed towards the white substance. The ganglion cells have a more or less conical form, the base of the cone being directed to the white substance, and sending forth a number of processes which quickly ramify, whilst the apex of the cone is continuous with a single longer, thicker, and at first unbranched process. In accordance with the observations of Meynert, however, I have seen this process, which has been compared to the axis-cylinder process, divide, sooner or later, in a dichotomous manner, and undergo further subdivision in cells which had been completely isolated by maceration in iodized serum. I have witnessed a similar division in the pedunculated ganglion cells of the Pes huffocampi major, respecting which Deiters ¶ was of opinion that the thicker process, constituting the stalk of the cell, was an axis-cylinder process. Nevertheless, I am unable to admit that either these cells or those of the gray cortex of the brain can, without further investigation, be classified with the multipolar cells of the spinal cord. Still it is quite true that the cells of the cerebrum, as I have already observed, possess an exquisite fibrillar structure, and rather appear as a point of junction and intersection for nerve fibrils that are already developed, than as a point of origin for those which have not hitherto been in existence.

In addition to the larger cells of the cerebrum which have just been mentioned, an enormous number of smaller cells are found in that organ, the nuclei of which are invested by only a small quantity of cell substance. It has been demonstrated that some of these give off processes, of which the ultimate destination is certainly not known, but which are, nevertheless, sufficient to characterize the cells as nerve cells, and to distinguish them from the connective tissue cells that are undoubtedly present in the spongy connective tissue of the central organs of the nervous system. Amongst these small cells, some are multipolar, some bipolar, and some unipolar. They form thick layers in the cerebellum, and both Gerlach** and more re-

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* *Archiv für Mikroskopische Anatomie*, Band iii., p. 441.

† *Vierteljahrschrift für Psychiatrie*, Bände i. and ii.

‡ *Loc. cit.*, p. 72.

§ *Mikroskop. Studien*, p. 11.

‖ *Handbuch der Gewebelehre*, 5. Auflage, 1867, p. 243.

¶ *Loc. cit.*, p. 66.

** *Mikroskop. Studien*, Taf. 2.

cently Franz Schulze* have shown that their processes consist of immeasurably fine fibrils. If we therefore venture to inquire into the central origin

Fig. 43.

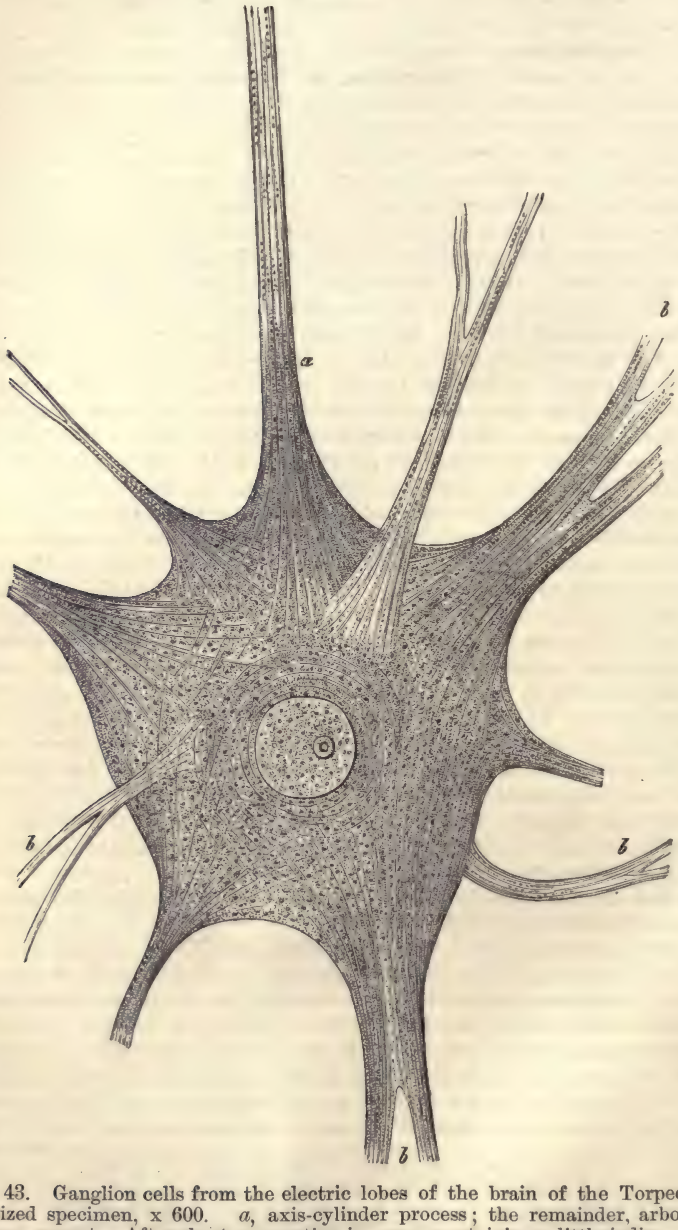

Fig. 43. Ganglion cells from the electric lobes of the brain of the Torpedo, medium-sized specimen, x 600. *a*, axis-cylinder process; the remainder, arborescent processes, recent. After short maceration in serum containing a little iodine.

* *Ueber den feineren Bau der Rinde des kleinen Gehirns*, "On the Minute Anatomy of the Cortex of the Cerebellum." Rostock, 1863, fig. 11.

of the primitive fibrils in the brain and spinal cord, which appear to exist already completely formed in the larger ganglion cells, we may suppose that it is from these extremely small and, in part at least, unipolar nerve cells, though it must be admitted that this is pure hypothesis. In the present state of our knowledge, however well we may be acquainted with the peripheric mode of termination of a great number of nerve fibrils, it cannot be said that the mode of central origin of any single fibril has hitherto been proved. We may, however, conclude from analogy that the central extremity is to be sought either in the cell substance of the nerve cells, or in the nucleus, or in the nucleolus. Observations have been made which render all these three modes of central termination of the nerve fibrils probable; but no perfectly satisfactory conclusion can be said to have been as yet attained on this point; and it is even conceivable, according to my observations, that there is no actual termination of the fibrils in the brain or spinal cord; in other words that all fibrils originate at the periphery, and thus only traverse the ganglion cells.

The question of the relation of the nerve fibres to the ganglion cells appears, from what has been stated above, to be still an open one on certain points. If the view long ago entertained, especially by Valentin, that the nerve fibres only coil round the ganglion cells, and do not enter into more direct connection with them, is opposed by the brilliant investigations of Remak and Helmholtz, still the question of the centric mode of origin of the nerve fibres has not yet been thoroughly solved. It is obvious that the mere interruption of a nerve fibre in some part of its course by a bipolar ganglion cell, as was so beautifully described and delineated by Bidder in 1847, affords no information respecting its centric origin. Such a ganglion cell is to be regarded as composed essentially of only a nucleated enlargement of the axis cylinder. If we pass to a more central portion of the nervous system, we meet with the multipolar ganglion cells of the spinal cord, or of the medulla oblongata, from which, according to the important discovery of Deiters, the axis cylinder of the fibre in question proceeds as an undivided process. The numerous other processes of the cell connect it, and by its means the axis cylinder, with more distant regions of the central organs, and probably also of the periphery of the body, but clearly do not entitle us to regard the ganglion cell as the exclusive origin of the nerve fibre. If we compare the axis-cylinder process with the stem of a plant and its divisions, and the peripheric terminal organs with the branches, leaves, and flowers, the ganglion cell is equivalent to the root stock, and the branched processes to the subterranean root fibres. It is requisite to follow these out in order to arrive at the extremity opposite to the peripheric termination. In consequence of the evidence I have adduced of the exquisitely delicate fibrillar structure of the ganglion cell substance, and of all its processes, a path is opened by which we may investigate the true central terminations of the fibrils entering into the composition of the axis cylinder. Unfortunately, the individual fibrils within the substance of the cells escape all accurate observation.

The above comparison of the ganglion cells and their processes with the root stock, stem, and root fibres of a plant, is, after all, like most comparisons, only an imperfect one. The branched processes of a multipolar ganglion cell, such, for instance, as may be found in the anterior horn of the spinal cord, have certainly not all been satisfactorily ascertained to pass as primitive fibrils to the axis-cylinder process; but rather this receives only a single group, the remainder extending as branched processes in other directions. Thus the ganglion cell constitutes a common point of union of numerous separate fibrils proceeding from widely different regions of the nervous system; and whilst one of these associated bundles becomes the axis cylinder of a fibre, and after becoming invested by a medullary sheath, immediately runs peripherically, the others pass in unknown directions.

It remains to consider whether, admitting that a large number of the fibrils are already formed, and only traverse the ganglion cells, there may not be some which do actually originate in these. In regard to this point, the interfibrillar granular substance is first to be noticed, which is probably a residue of the embryonic protoplasm, by the agency of which the fibrils are differentiated; a substance which possibly remains in greater abundance in the immediate vicinity of the nucleus, and there retains a power allied to that which it possessed when in the embryonic state. Yet, however probable it may appear that the several fibres arise in and from this substance,

no observations have as yet been made which establish it with perfect certainty. Another mode of origin of new fibrils or thicker fibres from the ganglion cells has, on the contrary, been suggested by various observers. Since Harless * stated that the nuclei and the nucleoli of the large cells of the brain of the torpedo were the points of origin of the nerve fibres, the same view has been entertained by many others in regard to other ganglion cells, and especially for those of the sympathetic of the frog, as in the first instance by Axmann, Lieberkühn, and Wagner, and subsequently by Beale, Arnold, Frommann, Jolly, and Courvoisier. But it was noticed by Frommann and Arnold † as occurring also in the cells of the spinal cord and in those of the brain; and Meynert stated that the nuclei and the nucleoli were centres for fibres, the fineness and delicacy of which render them comparable to our primitive fibrils. I agree with Kölliker and others, however, in the statement that this, at least, is not the ordinary condition, and I have not been more successful than Kölliker in obtaining any positive evidence of such a mode of origin of the fibres in question.

Although anastomoses occur between adjoining ganglion cells, it is a matter of much difficulty to acquire any certain information respecting the constancy or frequency of their occurrence. As there are ganglion cells with two nuclei, like those, for example, that, according to Guye and Schwalbe, are constantly met with in the sympathetic, and occasionally in the brain of the rabbit, so we may refer one form of the anastomoses occurring between ganglion cells to the type of bi-nucleated cells; those, namely, in which a short thick bridge unites two nucleated corpuscles with one another. Such anastomoses have recently been described by Meynert, R. Arndt, and Besser, as they are seen in the cortex of the cerebrum. They appear, however, to occur but rarely. The numerous anastomoses supposed to take place between the large ganglion cells in the nuclei of origin of various nerves in the spinal cord and medulla oblongata, and depicted amongst others by Schröder v. der Kolk and Lenhossek, have long been recognized as illusions. Other anastomoses between the ganglion cells of the various cortical layers of the brain, which are stated to occur by Meynert, require further corroboration. It is quite a matter of doubt whether we shall ever be able to observe those anastomoses between ganglion cells which result from the union of the finest outrunners of the branched processes, since the most carefully conducted methods of isolation adopted by Deiters have only led to negative results. Nor have my own numerous researches on the ganglion cells of the electric lobes of the torpedo, which are admirably adapted for this investigation, been more fortunate; for although Rud. Wagner long ago stated that anastomoses could here be distinctly seen, I, notwithstanding the employment of better modes of isolation, have been unable to discover a single instance of their occurrence. Lastly, an interesting accession to our knowledge of the terminations of the nerves may here be noted, with which I have become acquainted whilst these sheets were passing through the press. Paul Langerhans found, as he has described in Virchow's *Archiv*, Band xliv., p. 325, and depicted in the twelfth plate of that volume, that processes of the non-medullated fibres of the cutis in man penetrate between the cells of the rete Malpighii, exactly in the same way as has been described (p. 164) by Hoyer and Cohnheim as the mode of termination of the nerves in the cornea. These nerve fibrils, however, do not terminate by free extremities; but enter, as is rendered highly probable by Langerhans, in all instances, into small cells lying between the deeper cells of the rete mucosum, which again give off several fine fibrous outrunners into the upper layers; and these finally terminate with slightly clubbed extremities just beneath the horny layer. These nerve fibres have no connection with the tactile corpuscles. By means of these observations, which supplement those of Tomsa and others respecting the mode of termination of the nerves in the corium in several important particulars, the intimate connection between the terminations of the nerves and the epithelial layers in the skin of man has been demonstrated, which, since the year 1856, has been gradually shown to occur in all the other organs of sense, although it was in the first instance received with so much mistrust. Thus one more argument in favor of nerve plexuses representing the terminal structure falls to the ground.

* Müller's *Archiv*, 1846, p. 317, Taf. 10.

† Arnold, in Virchow's *Archiv*, Band xli., Taf. 4.

CHAPTER IV.

THE TISSUE OF THE ORGANIC MUSCLES.

By J. ARNOLD.

THE constituents of this tissue are fusiform contractile fibres, connective tissue, and cement, with vessels and nerves.

FORM AND GENERAL CHARACTERISTICS.—Fusiform fibres of this tissue are sometimes designated as smooth muscular fibres, or as contractile or muscular fibre cells; and when examined in an isolated and uncontracted condition, appear as sub-cylindrical fibres, generally with two or more flattened sides, and occasionally in the form of flattened oval plates. They for the most part resemble a spindle, being slightly swollen near the centre, and pointed towards each extremity (fig. 44); but the thickest part is frequently not quite centrally situated, being nearer to one end than to the other (fig. 45).

In many instances the extremities of the fibres are not single, but more or less divided, so that processes are given off from one or both poles; and in accordance with the depth to which the division extends, the length, form, and relative position of these processes vary (fig. 46). Thus, when the depth is slight, they are small, short, and more or less parallel to one another; when, on the other hand, it is considerable, they are long, broad, and diverge from each other almost at right angles. This forking of the muscular fibres occurs especially in those places where the fasciculi are arranged in the form of a network, and may properly be regarded as peculiar to this variety of the tissue. Such fibres, at all events, occur very frequently in the urinary bladder of the frog, at the points of intersection of the fasciculi.

The surfaces of the muscular fibres, as well as their borders, are generally smooth; the latter are, however, occasionally slightly serrated, and the former are sometimes uneven,—appearances which, like the curving of the ends, must be regarded as consequences either of manipulation in the preparation of the specimen, or as *post-mortem* changes.

Another explanation must, however, be given of the transverse striæ, which occur in considerable numbers, and at regular distances, on one or both sides of the fibres. These, from the concordant results of the observations of Meissner * and Heidenhain, † are probably to be regarded as phenomena of contraction.

The length of the fibres varies from 0·045—0·230 millimetres; the mean length is from 0·084—0·089 millimetres; the breadth 0·004—0·01 millimetres.

STRUCTURE OF THE SMOOTH MUSCULAR FIBRES.

The substance of the muscular fibre cells examined in serum whilst perfectly fresh has a dull appearance, except at the edges, which are frequently somewhat clearer. In many specimens no further indications of structure

* *Zeitschrift für rationelle Medicin*, Band ii., 1858.
† *Studien des Physiologischen Instituts*, 1861.

are perceptible, but in others there is a more or less distinct longitudinal striation, which is often particularly obvious near the extremities, and is rendered still clearer by the addition of a few drops of a 0·01 per cent. solution of chromic acid, or of solution of gold containing 0·1 per cent.

Fig. 44.

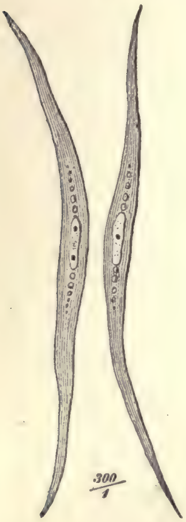

Fig. 45.

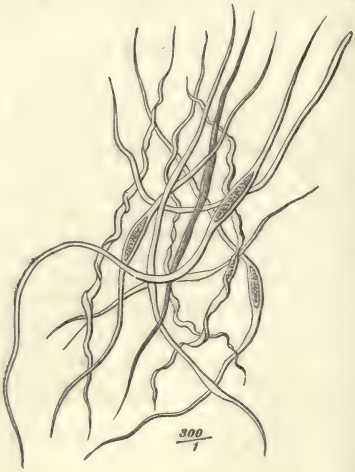

Fig. 46.

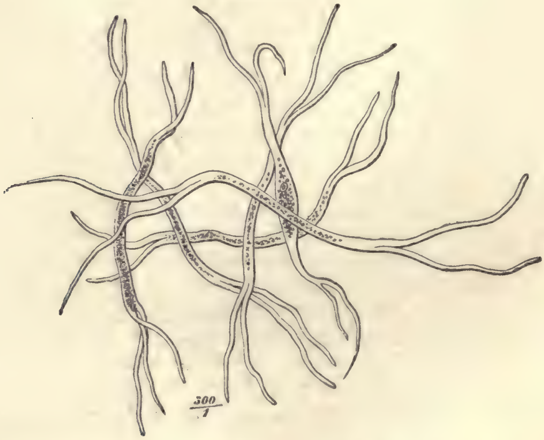

Fig. 44. Muscular fibres treated with serum. Fig. 45. Muscular fibres from the muscular tissue of the intestine, isolated by means of nitric acid. Fig. 46. Dichotomously divided muscular fibres from a pleuritic membrane.

(fig. 44). In many fibres, dark, highly refractile granules are imbedded in various parts, apparently without any definite arrangement. These, which disappear on the addition of alcohol, are not to be confounded with the granules that are commonly found at the two ends of the nucleus. The latter form pyramidal rows extending for a greater or less distance from the

poles of the nucleus to which their bases are applied towards the ends of the fibres to which their apices point. These granules are imbedded in a substance which has likewise the form of a pyramid, and is differentiated from the adjoining material by its greater transparency when examined by transmitted light. In many fibres a second line is to be observed, which lies at some distance from, and not quite parallel to, the margin. This forms the line of demarcation between an external darker and an internal clearer and brighter layer. A similar differentiation of parts may be discerned on examining the transverse section of a fibre in which the cortical layer appears as a dark ring investing the remaining brighter portion. The outer contour of this is always distinctly marked, but its inner is never very sharply defined. The thickness of the cortical layer varies, and in many fibres it is altogether absent.

Margo * gave a description of certain small points arranged serially in the interior of the fibre cells, and separated from each other by minute intervals; whilst Wagener † first described the distinct longitudinal striation that gives the impression of a fibrillar arrangement near the extremities of the fibres. The rows of granules extending from the poles of the nucleus were first mentioned by Klebs,‡ and subsequently by Frankenhäuser § and Wagener. ‖

NUCLEUS.—*General form and size.*—The nucleus of the fibre cells is generally single, very rarely multiple, always distinctly rod-shaped, and either rounded at the ends or pointed. It is occasionally curved or spirally convoluted. On transverse section the nucleus appears either round or subangular. It invariably occupies the fusiform enlargement of the fibre, but its position in regard to the transverse diameter is less constant, since on section it is sometimes seen to lie in the middle of the ring formed by the transverse section of the fibre, and sometimes near the margin. Moreover, the nucleus sometimes lies obliquely in relation to the axis of the fibre cell. The length of the nucleus varies from 0·015—0·022 millimetres, and its diameter from 0·002—0·003 millimetres.

STRUCTURE OF THE NUCLEUS.—In perfectly fresh muscular fibres treated with serum the nucleus may indeed be perceived, but its contour is not very well defined; on the addition, however, either of chromic acid (0·01 per cent.), acetic acid (1 per cent.), or solution of chloride of gold (0·1 per cent.), the contours become sharp and dark, whilst the previously homogeneous contents appear finely granular. In the substance of many nuclei, especially when treated with serum and chloride of gold, but less distinctly with acetic acid, there may be observed from two to four large (from 0·001—0·002 millimetres) highly refractile round granules (fig. 44). If one only be present, it lies near the centre, or frequently somewhat nearer to one of the poles of the nucleus. If, on the other hand, two are present, they are situated at the two ends of the nucleus. These granules are most distinct in transverse sections of the nucleus, and are then seldom absent. They

* *Neue Untersuchungen über die Entwickelung, das Wachsthum und den Bau der Muskelfasern*, "Recent Investigations on the Development, Growth, and Structure of Muscular Fibres," 1859.

† *Sitzungsberichte der Gesellschaft zur Beförderung der gesammten Naturwissenschaften*, No. 10, 1859.

‡ Virchow's *Archiv*, Band xxxii., 1865.

§ *Die Nerven der Gebärmutter und ihre Endigungen in den Glatten Muskelfasern*, "The Nerves of the Uterus, and their Mode of Termination in smooth Muscular Fibres," 1867.

‖ *Loc. cit.*

may also be perceived in association with isolated nuclei, and in such cases they either lie close to the surface of the latter, or project more or less from its margin.

Frankenhäuser * has paid particular attention to the structure of the nucleus ; and although Hessling † had previously noted the existence of a nucleolus in the interior of the nucleus, Frankenhäuser first stated that it was an essential and a never-failing constituent. Piso-Borme ‡ also observed the presence of nucleoli.

Connection and Arrangement.—The contractile fibre cells are united into fasciculi or membranes of various size, through the intervention of a connecting material. The fibres are so arranged that the ends of two or more are inserted between the diverging extremities of two which touch at their dilated middle portion, an arrangement by which an intimate union of the several structures is effected. In cases where the greater number of the fibres are superimposed by their flat surfaces, a membrane is formed, consisting of one or many layers, the fibres for the most part preserving the same direction in each layer, though they may pursue very different direc-

Fig. 47.

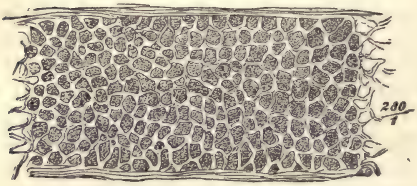

Fig. 48.

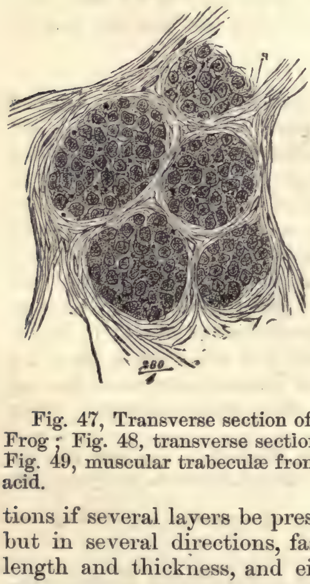

Fig. 49.

Fig. 47, Transverse section of the longitudinal fibrous layer of the intestine of a Frog ; Fig. 48, transverse section of muscular bundles from the uterus of a Sheep ; Fig. 49, muscular trabeculæ from the urinary bladder of a Frog, treated with acetic acid.

tions if several layers be present. Where the fibres are united, not in one, but in several directions, fasciculi of fibres are produced. These vary in length and thickness, and either run parallel to each other, or cross at a

* *Loc. cit.*
† *Gewebelehre*, 1866.
‡ Moleschott's *Untersuchungen*, Band ix., 1860.

more or less acute angle, or, lastly, present a plexiform arrangement, and frequently anastomose. It is from these differences in the directions taken by the fibres, and in their mode of union, that the irregularities observed in section result. For if the section be carried transversely through a portion of the tissue in which the muscular fibres run parallel, round or subangular rings, lying in close proximity, are met with, presenting a central or laterally situated transversely divided nucleus; whilst if the bundles of fibres run in various directions, transverse and oblique sections of the fibres and nuclei appear (figs. 47 and 48). The quantity of connecting substance is sometimes very sparing, so that the surfaces of the fibres are in almost direct contact, or are separated only by very thin layers or columns of the connecting substance. Occasionally, however, it is more abundant. In the former case the muscular fibres appear, on transverse section, as closely compressed polygonal areas; in the latter, as roundish spaces, between which are more or less broad laminæ of the connecting substance. This material is homogeneous, except that it contains numerous pale branched cells, the processes of which intercommunicate, and also a moderate number of dark, highly refractile granules, 0·001 to 0·002 millimetres in diameter, which are always visible. They sometimes lie in the centre of the connecting material, sometimes close to the borders of the spindle-like expansion of the fibre cells. They closely resemble the granules of the nucleus. In specimens treated with solutions of chloride of gold they present a dark violet tint, and are always much darker than other parts of the connecting substance (fig. 49).

Both the muscular fasciculi and the membranous expansions are invested both externally and internally by connective tissue, which, for the most part, is distinctly fibrillar, and contains loose fibres of connective and elastic tissue. By means of this the several laminæ are united into a membrane, and the fibres into fasciculi. The latter are sometimes so combined as to form a tough, dense, flattened or roundish mass, which, as Treitz* has shown, fulfils the office of a tendon.

Vessels.—The layers of the connective tissue investing the fasciculi and membranes of organic muscular tissue, are traversed by numerous arteries of various size, which break up into a network of capillaries, from which again the veins take origin. These, like the arteries, run in the investing connective tissue; but the capillaries penetrate the muscular layers. The meshes of the capillary plexus are of moderate width, and are sometimes elongated, and at others round or rhomboidal. The vessels themselves present no important peculiarities.

Nerves.—In all organs or part of organs, in the composition of which the organic muscular tissue plays an important rôle, and apart from differences occurring in particular instances, a similar arrangement of the nerves is to be found. The different nerve fibres contain a variable number of dark-edged and pale nerve tubules. Of these, the former present the features characteristic of the medullated fibres, vary in size, and are usually the most abundant. There are, however, a few fasciculi, which chiefly consist of the pale fibres, and contain but a small number of the dark-edged variety. The former appear as fine glistening filaments, of from 0·0018 to 0·0023 millimetres in breadth, with here and there a nuclear enlargement of 0·003 to 0·005 millimetres in diameter, a peculiarity which at once enables

* *Prager Vierteljahresschrift*, Band i., 1852.

them to be distinguished from even the finest doubly contoured fibre. The fasciculi thus composed of pale and dark-edged fibres, lie in the connective tissue surrounding the muscle bands or membranes, and form wide-meshed flat plexuses, in which the adjoining fibres cross and interchange from one plexiform layer into another. In the plexus formed by the larger nerves (*principal or foundamental plexus*) ganglion cells lie scattered, which are often collected into microscopic ganglia; and from the same plexus fibres are given off, which are at first dark-edged, but subsequently assume the form of broad pale bands. These present a fine longitudinal striation, with nuclei at various distances, which are sometimes smaller than the fibres, and at others cause their edges to project. The pale fibres are from 0·004 to 0·005 millimetres in breadth, and their nuclei have about the same diameter. After running for a certain distance they rapidly diminish in size, and split into finer glistening fibres, which have nuclear enlargements and a diameter of from 0·0018 to 0·0023 millimetres, and are similar to those contained in the fasciculi. These fibres form plexuses with meshes of moderate size, and of rhomboidal or elongated shape. Bodies resembling nerve cells or nuclei with distinct nucleoli occupy the points of junction. Pale fibres, proceeding directly from the main or fundamental plexus, enter into this plexus. The network of pale fibres, just described, lies immediately upon or beneath the muscular laminæ, embraces the muscular bundles, and probably intercommunicates freely with the fibres proceeding from the fundamental plexus to form an *intermediate plexus* (fig. 51). In the larger muscular fasciculi, portions of the intermediate plexus are sometimes found within the layers; but in general the arrangement above described is that which obtains. Fine fibres are given off from the intermediate plexus, which penetrate between the muscular fibres, and at the points of division still present nuclear enlargements, though these are subsequently absent, the fibres at the same time becoming rapidly attenuated (fig. 50). After they have undergone repeated division, they appear as fine, cylindrical, dark filaments, of from 0·0003 to 0·0005 millimetres in diameter. These contain, both in their course and at their points of division, dark granules of round, elliptical, or polygonal form, which, by their somewhat larger size (0·001 to 0·0018 millimetres) and brighter appearance, serve to indicate the course of the fibres (figs. 50 and 51). They are tolerably distinct in preparations moistened with serum; but, as has already been stated in the description of the connecting substance, the delicate plexus formed by the fibres is not very perceptible without the addition of other reagents. The delicate fibres bearing nuclei, which have just been described, unite with one another to form very delicate networks, which traverse the connecting substance occupying the interstices of the muscular fibres, and are seen winding round the fibres in the form of delicate dark lines, interrupted with nuclear enlargements, and constitute the *intra-muscular plexus*. Transverse sections of frozen portions of muscle treated with serum and chloride of gold permit these fine nuclei-bearing fibres, with their relations to the connecting substance on the one hand, and with the muscular fibres on the other, to be readily perceived (fig. 52). From the intra-muscular plexus, and chiefly in the vicinity of the spindle-like enlargements of the muscular fibres, dark peculiarly stiff filaments proceed, having a diameter of 0·00015 to 0·0002 millimetres. These penetrate into the interior of the fibres, and extend towards the nucleus. Several of these filaments, or one only, in accordance with the number of granules in the nucleus, may penetrate the muscular fibre from different sides; but, whatever may be their number, they all pass towards the granules of the nucleus, which might therefore be regarded as

Fig. 50.

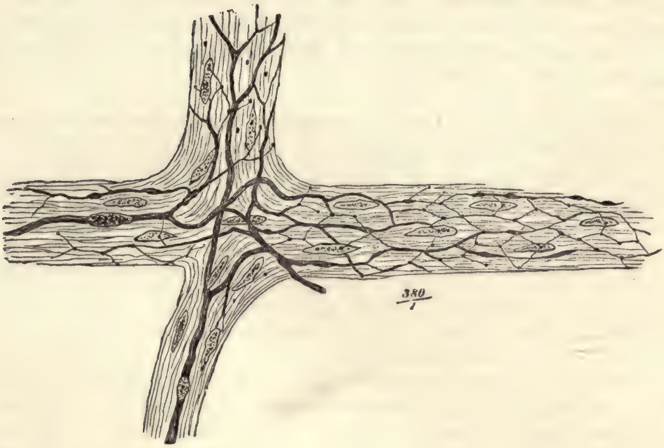

Fig. 51.

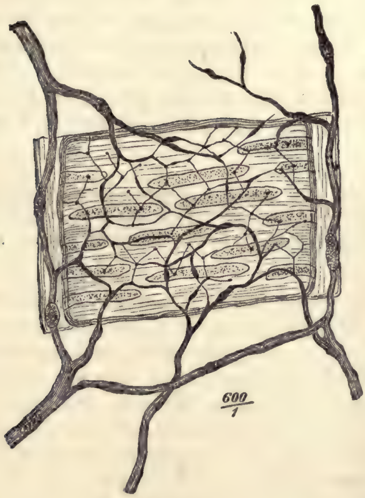

Fig. 52.

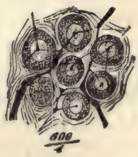

Fig. 50. Nerve ramifications and terminations in a muscular fasciculus taken from the urinary bladder of the Frog (prepared in chloride of gold solution). Fig. 51. Nerve ramification in the muscular coat of a small artery (prepared in acetic acid, 1 per cent., and chromic acid, 1-100th per cent.). Fig. 52. Ramification of the nerve as shown on a transverse section of muscular fasciculi from the uterus of a Sheep. (The section was made from a portion of frozen muscle which had afterwards been treated with 0·01 per cent. of chromic acid.)

the extremities of the fibres, were it not that in many cases they again gave off filaments, which, traversing the substance of the nucleus and of the muscular fibre in the opposite direction, enter the intra-muscular plexus. Consequently these granules are not the free ends of the smallest nerve fibres, but only the nodal points of the finest nerve plexus lying within the nucleus. The best demonstration of these relations also is to be obtained from transverse sections (fig. 52).

After Klebs* had in the first instance recognized that an intimate relation existed between the finest nerve filaments and the substance of the muscular fibres, it was shown by Frankenhäuser † that the former penetrated into the interior of the latter, and proceeded to the granules of the nucleus, to which he applied the name of nuclear corpuscles (Nucleoli, Kernkörperchen). The statements above made are the result of careful investigations which I have elsewhere more fully reported. As regards the relations of the finest nerve filaments to the substance of the muscular fibre and its nucleus, as well as to the intra-nuclear granules, I coincide with Frankenhäuser. On the other hand, I was unable to recognize the actual extremities of the nerve fibres in the granules of the nucleus; they rather appear to me as nodal points of the finest nerve plexus lying in the interior of the nucleus.

Distribution.—Smooth muscular fibres are widely distributed through the body. In the organs of respiration they are seen to form layers of circular fibres in the posterior wall of the trachea, and in the bronchi. Their presence in the walls of the alveoli of the lungs in man and mammals is still doubtful, being admitted by some observers, whilst it is denied by others. Muscular fibres are, however, certainly present in the alveoli of the lungs in infants, and in the lung-sacs of the frog, salamander, and triton.

In the alimentary canal, smooth muscular fibres form membranes, which are to be found from the lower part of the œsophagus to the extremity of the large intestine. They also form a proper layer in the mucous membrane, the so-called *muscularis mucosa*, and in the small intestine extend from thence into the villi. The excretory ducts of many glands possess a proper muscular layer, as may be seen in the pancreatic duct of the Ox, Cat, Pigeon, and Carp.

According to Tobien, the ducts of all the salivary glands contain muscular fibres; but Kölliker only saw a few in Wharton's duct, and Henle but a few in Steno's duct; whilst, according to Eberth, they are not present in the ducts of the salivary glands generally.

Smooth muscular fibres are also found in the lymphatic glands, and in the spleen. Opinions are, however, divided in regard to the distribution of the muscular tissue in the latter. In man, muscular fibres are contained in the capsule of the spleen; and some also maintain that they are present in the trabeculæ. The quantity of smooth muscular fibres in the capsule of the spleen in various animals differs to a considerable extent. They are very abundant in the porpoise, hedgehog, dog, cat, pig, mole, rat, and rabbit, but exist only in small quantity in the ruminants and in apes. In the pig, dog, ass, sheep, rabbit, horse, hedgehog, guinea-pig, peccary, bat, and cat, again, nearly *all* the trabeculæ contain muscular fibres; but in some, as the ox, these fibres are only present in the more delicate trabeculæ. Smooth muscular fibres are also found in the walls of the gall-bladder, in the cystic duct,

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* *Loc. cit.*

† *Die Nerven der Gebärmutter und ihre Endigungen in den Glatten Muskelfasern*, "The Nerves of the Uterus, and their Mode of Termination in smooth Muscular Fibres," 1867.

and in the ductus communis choledochus. They constitute an essential portion of the middle coat of the vessels; they form connected laminæ and membranes in the parietes of the calyces and pelvis of the kidney, and of the ureters and urinary bladder. They are found beneath the mucous membrane of the prostatic and membranous portions of the urethra, both in the male and female. Smooth muscular fibres are widely distributed in the male sexual apparatus, entering into the composition of the vas deferens, the vesicula seminalis, the prostate, the corpora cavernosa, Cowper's glands, and parepididymis; between the tunica vaginalis communis, and propria, and in the dartos. In the female sexual organs it occurs in the oviducts, in the broad and round and in the anterior and posterior ligaments of the uterus. It is by far the most important constituent of the uterus. In the vagina it forms an actual muscular membrane. Its presence in the ovaries, whilst admitted by some, is denied by others. Numerous smooth muscular fibres are found in the nipple and in the surrounding areola, also near the hair follicles, where they have received the name of arrectores pili; and in the sebaceous and sweat follicles. Finally, the presence of smooth muscular fibres in the ciliary muscle, effecting the contraction and dilatation of the iris, is to be noted, and I may also refer to the discovery of smooth muscular fibres in the membranes of the egg.

Methods of Investigation.—The more delicate points in the structure of organic muscular fibre are best demonstrated in preparations that have been treated with serum, chromic acid (0·01 per cent.), and solution of gold (0·1 per cent.). The urinary bladder, lungs, and smaller arterial vessels of the frog may be particularly recommended as forming good material for examination; but for the isolation of the individual fibres without the application of any reagents, the muscular tunics of the intestine are most appropriate. The means usually employed to effect the separation of the elementary fibres are acetic acid diluted with from 3 to 5 per cent. of water, nitric acid (20 per cent.) and solutions of potash (32 per cent.), all of which act in the same way by dissolving the connecting substance, and thus enabling the muscular fibres to be isolated. Maceration in iodized serum, and in dilute chromic acid (0·01 to 0·05 per cent.), is in some cases very effective. For the preparation of transverse sections, alcohol, chromate of potash, and chromic acid—the last two being employed alternately—constitute excellent hardening agents. If it be desired to examine the muscular fibre in as fresh a state as possible, transverse sections may be prepared from frozen portions of muscle, which have then been placed in serum. Such sections are, moreover, well adapted for being treated with gold, silver, and dilute chromic acid solutions. The course and termination of the nerves are distinctly seen in preparations macerated for from two to four minutes in 4 cub. centim. of a solution of acetic acid, containing from 0·5 to 1 per cent., and then for half an hour or more in 4 cub. centim. of a 0·01 per cent. of chromic acid. Besides this combined action of acetic and chromic acids, I can also recommend acetic acid and alcohol both for the investigation of gold preparations and of sections treated with solutions of gold and chromic acid. The best materials are the urinary bladder and the smaller arteries of the frog. For treating the sections, carmine, anilin, chloride of palladium (F. E. Schulze), and picric acid (Schwarz) may be employed.

CHAPTER V.

THE MODE OF TERMINATION OF NERVE FIBRE IN MUSCLE.

BY W. KÜHNE.

WE exercise control over our muscles through the agency of the nerves, and it is through the nerve paths alone that the will excites them to contract. The question therefore naturally arises, In what way do nerves terminate in muscle? Inquiries were made on this point long before instruments and modes of investigation could furnish any answer, and these led to ever new and ever unsatisfactory researches.

We now believe that we are able to perceive the direct continuity of the contractile with the nervous substance. Yet it may still happen that, in consequence of further improvements in our means of observation, that which we regard as certain may be shown to be illusory. Nevertheless, work is indispensable, and we must press on till we reach the point in the domain of morphology, in which order and law become the last expression of our knowledge. Up to the year 1840 all attempts to give a satisfactory account of the ultimate termination of the motor nerves failed. The admission of loop-like extremities in the muscle can only be regarded as an expression of ignorance, and of the impossibility of following the course of the nerves in muscle with clearness.

But suddenly and accidentally an unprejudiced observer, in investigating the interesting small Tardigrada, recognized nearly all that we know at the present time regarding the ends of the motor nerves. In 1840, Doyère discovered that the nerve applied itself to the muscular fibre by means of a conical enlargement. Both of these structures are destitute of sheaths or investing membranes in the Tardigrada (or bear animalcules), and the nervous and muscular tissues thus come into direct contact.

The observation of Doyère long remained misunderstood, and passed into oblivion in consequence of the general acceptance of the view of Ernst Brücke and Joh. Müller, to the effect that the primitive nerve fibres undergo division between the muscular fibres. It was, indeed, completely forgotten when R. Wagner recognized with much discrimination the value of that mode of nerve termination which Savi first discovered in the electrical organs of the Torpedo, and applied it as a fact of general significance to all peripherically distributed nerves. It then first became intelligible how so small a number of nerve fibres as those which are ordinarily contained in a motor nerve can influence such a much larger number of muscular fibres. In a carefully written essay, Reichert showed that the pectoral cutaneous muscle of the frog, which is composed of about 160 muscular fibres, receives only about six or seven primitive nerve fibres; but the proportion was no longer unintelligible when far more, in fact nearly 300, terminal fibres, proceeding from the division of the latter, could be proved to be present. Of these investigations, however, few or none were directed to the solution of the question respecting the proper termination of the nerves, but rather to their mode of division between the muscular fasciculi. The latter point lies beyond the limits of the present paper, and we shall there-

fore content ourselves with the description of what is of most importance in regard to it.

When thin transparent muscles or thin sections of muscles are examined, nerves of varying degrees of fineness may be seen, the course of which is seldom parallel, but frequently at right angles, to the direction of the fibres of the muscle. This is especially noticeable in regard to isolated nerve fibres, and to the terminal portions of such fibres. The muscles of different animals, and even the several muscles of the same animal, are very unequally supplied with nerves. In a few of the lower animals, as in Bowerbankia, the muscles appear to possess as many nerve as muscular fibres; in others, especially in Fishes, there are surprisingly few, whilst amongst the warm-blooded Vertebrata the muscles of the eye, as a general rule, contain but few more muscular fibres than primitive nerve fibres. If we start with the assumption that every muscular fibre must be supplied with at least one nerve fibre, even if this be the result of division, it is obvious that the muscular apparatus of Fishes, divided as it is to so great an extent by tendinous intersections, and which, as a consequence of the shortness of these fibres, contains in an equal volume many more individual muscular fibres to be supplied with nerves, than the long-fibred muscles of other classes, can receive only a smaller number of primitive nerve fibres. The Fish would indeed have to carry a weighty mass of nerves, were the relation between the two tissues the same as in mammals. Hence, nowhere are so many divisions of the primitive nerve fibres to be so easily found as in the muscles of this class.

The large relative number of nerves distributed to the ocular muscles, and generally present in all the muscles of Mammals, but as it would appear especially in the muscles of man, is very suggestive in regard to the exact regulation of their movements, for the uncommonly fine adjustment of the ocular muscles would be unattainable if the excitation of one nerve fibre had as a consequence the excitation of as great a number of muscle fibres as in the Frog, and still more as in the Fish. In regard to the general distribution of nerves, allusion may here be made to the well-known fact that considerable segments of every muscle may be met with in which no nerves are to be found, and that in particular the extremities of the muscles appear to be destitute of nerves for a considerable space. The muscles that are best adapted for the study of the mode of division of the nerves supplying them, are the musculus cutaneus pectoris of the frog, and also the sartorius, the ocular and digital muscles, and the hyoglossus of the same animal; the ocular muscles of the fish, and amongst mammals those of the cat, and, above all, the thin muscles which extend from the vertebral column to the skin in the snake. These may be examined almost whilst yet still living, and merely flattened by a covering glass, or after being rendered transparent by means of a 1 per cent. solution of hydrochloric acid.

After the discovery of Doyère had shown the mode of connection of nerves without sheaths, with similarly naked muscular bands, the question naturally arose from a purely morphological point of view, whether transversely striated muscle, which is invested by a sarcolemma, and to which only nerves provided with sheaths are distributed, does not at some point allow the passage of these through the membrane. Still more strongly was the hypothesis respecting the continuity of the sheath of Schwann with the sarcolemma, or in other words, of the passage of the nerve fibre directly into the contractile substance, advanced by physiologists, thus leading the way to the establishment of all that has been discovered respecting the termination of motor nerves since the time of Doyère.

We shall commence with the transversely striated muscles, proceeding from the lower to the higher groups of animals, and leaving on one side, for the present, the relations existing in the unstriated fibres, and the still very incompletely known but apparently smooth muscular fibres of the worm, and other still more lowly organized Invertebrata.

The Mode of Termination of the Nerves in Invertebrata.

The striated muscles of the Articulata consist of completely closed cylindrical tubes of sarcolemma, the contents of which present the well-known appearance of a stage or ladder-like arrangement of superimposed disks of muscle prisms.* The muscle prisms are separated from each other in the transverse direction by a considerable amount, and in the longitudinal by a small amount, of homogeneous fluid material. All muscles, moreover, contain, besides those constituents which form the really contractile substance of the muscle, still another material that has some, though a less important influence on the development of force. It is generally regarded as the remains of the original formative cells of the muscle, and is composed of nuclei with a distinctly double-contoured membrane, and transparent contents, often with nucleoli; of vesicles of various form, without definite investment; of granules; and lastly of a finely granular pappy mass. These masses may be variously distributed in the interior of muscles, sometimes appearing in the form of a few short striæ, scattered through all parts of the fibre; sometimes as long bands lying between the contractile substance and the sarcolemma; and often, also, filling the interior of a canal running through the whole length of the fibre. In many instances the muscles of Crustacea present these masses in the form of a complete cylindrical tunic lying between the sarcolemma and the muscular substance. The masses may again be entirely isolated, or may communicate through the entire muscular fibre; those which lie in the central canals sending off radial processes which run towards the surface to join with the superficial portions, whilst in those which lie immediately beneath the sarcolemma, the processes extend towards the extremities of the fibres, and thus come into contact with others.

The most appropriate objects for the examination of the mode in which nerves terminate, appear to be the muscles of insects, and amongst these the best are the muscles of the great black water beetle (Hydrophilus piceus), which is to be preferred to the nearly allied Dytiscus marginalis. Instead of the muscles of the legs, it is better to employ the large colorless fasciculi lying in the thorax, which are attached by broad processes to the internal wing-like apodemata of the coxæ. If the muscle be suddenly separated from both its attachments by scissors, we obtain a preparation which, either without any addition, or merely with the addition of a little of the blood of the beetle, or a drop of 0·5 per cent. solution of chloride of sodium, will present, after gentle manipulation with needles, many beautifully isolated muscular fibres. These fibres are quite free from connective tissue, and are only bound together by nerves and tracheæ, both of which can be torn across with the greatest facility. Amongst the nerves many extraordinarily thick primitive fibres are to be found, invested by a distinct membrane, beneath which are very pale vesicular, and in parts also very finely granular medullary sheaths, whilst the axial portions present a fibrillar structure. The thick nerve fibres undergo repeated division, rivalling in this respect the

* The term "disks" was introduced into the description of muscle by Mr. Bowman. The same parts were designated by Rollett "chief-substance disks." The muscle prisms have been also, after Mr. Bowman, termed "sarcous elements."

ramifications of the bloodvessels of higher animals, and send off finer and still finer branches to the muscular fibres, each of which contains an extraordinary number of ultimate terminations. It may then be observed that the middle portions of the muscular fibres, at all points of their circumference, present rows of funnel-shaped processes forming little eminences of various size, the apices of which correspond to the points of entrance of the several branches of nerves. The latter appear in all instances to consist only of *a single axial fibril or axis cylinder;* but this may usually be seen to divide into two strongly diverging branches immediately beneath the apex of the nerve cone or eminence, and it may also be followed for a short distance into the interior of the eminence.

Fig. 53.

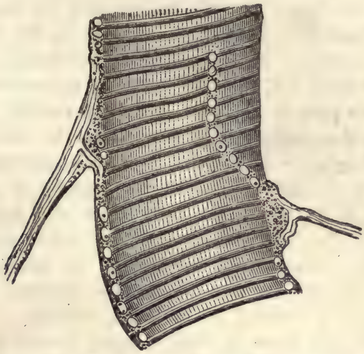

Fig. 53. Muscular fibre, with the extremities of two nerves, from the Hydrophilus piceus.

At the termination of the nerve the medullary layer, which has previously become extremely pale, entirely disappears; the image of the sheath of the nerve, therefore, where it joins the muscle, is not in the slightest degree obscured. It is impossible for the observer who sees this to doubt that the nerve sheath becomes continuous with the sarcolemma, and that the contour of the latter, as it rises towards the cone, or extends over the eminence, is directly continuous with the nerve sheath; or, in other words, that the nerve sheath and the sarcolemma form two communicating tubes. In whatever mode the nerve terminations may be presented to the eye, whether in a transverse section of the muscular fibre, or in the optic transverse section which is seen if a bent muscular fibre presents its convexity to the observer, he will still be constantly led to the same conclusion. The forms that the nerve eminence may assume are very various, sometimes constituting a pointed cone, at others a low rounded elevation, whilst in others, again, it is almost flat,—varieties that are doubtless attributable to the traction which has been exerted in the nerve in the preparation of the specimen. Nevertheless we may sometimes see, if not the pointed limpet-like cones, yet elevations of considerable height on muscular fibres, whose nerves have not been disturbed, as well as in flat portions of muscles which have been removed from the surface with scissors. We may therefore apply the general term of nerve eminence to the whole nervous expansion at this point, and honor its discoverer by naming it the Doyèrian eminence. Wherever a nerve terminates, it will be found that the contractile substance is covered beneath the nerve eminence with the secondary consti-

tuents of the mass; that is, with nuclei, granules, molecules, and the like. This relation is perfectly intelligible in the case of those muscular fibres which possess an entire investment of this substance; but it is also found where the chief striæ of it do not lie immediately beneath the sarcolemma, but are present as a central axis only, in which case the latter forms a conical projection, that passes transversely through the contractile substance, and nearly reaches the apex of the Doyèrian eminence. In other cases, where elongated small masses are found immediately beneath the sarcolemma, these lose their otherwise straight form, and bulge upwards towards the nerve eminence. The eminence has in some instances only a single process, running in a longitudinal direction from its basis, but more frequently there are two, which pass in opposite directions. The termination of the axis cylinder in the eminence, and its usually forked division, does not appear to have been clearly recognized by the greater number of observers. Rouget considers that it terminates in the Crustacea in a blunt point at the line of junction of the granular nucleated mass with the contractile substance; whilst in Beetles, after a somewhat longer course, it terminates at the same point. It will not be possible, without further investigation, to decide the question in regard to the final disposition of the axis cylinder; for, however probable Rouget's statements respecting the form that the process of the axis cylinder possesses may be, the position which he ascribes to it is, upon grounds that will hereafter be discussed, certainly surprising. The method of staining with solutions of gold and silver, which has been found so advantageous in other departments of the minute anatomy of the nerves, has up to the present, so far as this question is concerned at least, yielded no decisive results.

From what has already been stated it may, however, be maintained, in regard to the Arthropoda, that each of their muscular fibres receives a greater number of nerve ends; that the nerve sheath is continuous with the sarcolemma; that the proper conducting nervous fibre, that is to say, the axis cylinder, traverses the point of union of the two tubes, and divides in the nerve eminence; and that all nerve eminences possess at their base a layer of protoplasmic muscle substance, that may stretch to a variable extent into the contractile part of the fibre. These results have been obtained from an examination of the tissues in Hydrophilus piceus, Dytiscus marginalis, Carabus auratus, Silpha obscura, Melolontha vulgaris, Geotrupes stercorarius, Trichodes apiarius and alvearius, Musca domestica, Tabanus bovinus, Bombus, Tegenaria, Argyroneta aquatica and Astacus fluviatilis, and consequently in all three classes of the Arthropoda.

The Mode of Termination of the Nerves in the Vertebrata.

A. *Amphibia.*—The knowledge of the mode of termination of the nerves in Amphibia, and especially in the Frog, is of great interest, because these animals have for so long a period been employed by physiologists as the subject of investigation in regard to the relations existing between motor nerves and muscles. The different muscles of the Frog which have been particularly examined are the sartorius, the muscles of the eye, the short fibres of the penniform gastrocnemius, and the small muscles of the foot that lie between the toes.

The uncontractile protoplasmic substance, or the remains of it, in the muscles of Frogs, occupies, as is well known, a very inconsiderable space, as compared with the transversely striated contractile material. The muscle fibres are, indeed, dotted with nuclei, which are found not only imme-

diately beneath the sarcolemma, but in all parts of the transverse section; yet the protoplasmic portion is very small in quantity, and exists only in the form of a few molecules at the poles of the nuclei, or may even be altogether absent. Without methodical investigation it is almost impossible to strike upon the precise point in the fibres of the muscles of a frog which displays the mode of attachment of the nerve. This is sufficiently shown by the fruitless results of the observations repeatedly made antecedently to the last ten years.

After the experience that had been obtained respecting the connection of the nerves with the transversely striated muscular fibres invested with sarcolemma of the Invertebrata, it was somewhat more than an hypothesis when it was maintained that the conditions must be essentially similar in all animals in which nerves induce the act of contraction, and consequently in the Vertebrata. In order to decide whether every muscular fibre is connected with at least one nerve fibre, it was requisite to isolate the former in its whole length, and to examine its entire superficies. This was effected by the mode of isolating the fibres, suggested by Budge, through the agency of a mixture of chlorate of potash and nitric acid,—a plan that was advantageously modified by V. Wittich, who recommended that the muscle should be warmed with a very diluted solution of the same mixture. It is still better to soften the intermuscular connective tissue by maceration for twenty-four hours, in an extremely dilute solution of sulphuric acid, and subsequently to convert it into gelatine and effect its solution by warming it for a few hours at 104° Fahr. The isolation of the muscular fibres may then be accomplished by vigorous agitation with water in a test tube. By this method any muscle can be completely broken up into its individual fibres. The capillaries, which still often remain attached, must be removed by pencilling with a camel-hair brush. On carefully examining such isolated muscular fibres throughout their whole length, one spot at least may always be found to which a nerve fibre, usually more or less ramified, cleaves. In long muscles—as, for example, the sartorius—many fibres may be found which present several such spots, whilst in the shorter fibres of the gastrocnemius, as a rule, only one nerve eminence is visible. In specimens prepared in this way the continuity of the nerve sheath of Schwann with the sarcolemma may be observed in profile, without any further manipulation.

In order to bring the termination of the nerves in the fresh, still living, and contractile muscle into view—as in the Arthropoda—the fibres of the gastrocnemius are to be isolated. In the broken-up and separated muscle the course of the finest nerve twigs, as they cross the fibres at right angles, may be followed without difficulty by the pigmented vessels that accompany them. In this region the terminal branches are given off; and if a few muscular fibres are raised with the forceps, after the tendinous fasciculi to which they are attached have been divided at both extremities, in all probability the desired appearances will be presented to the eye. The specimen so obtained may be examined, either without any addition or in a 0·5 per cent. solution of chloride of sodium, in which the muscle long retains its excitability. The aqueous humor and the serum of the blood of the frog may also be employed. Just before the nerve traverses the sarcolemma it usually undergoes division, forming the so-called terminal brush (leash or pencil) of the nerve, the extremely short branches of which seldom exceed in length the transverse diameter of the muscular fibre, and may lie in all conceivable directions to its axis. The number of branches of the first order rarely exceeds five; those of the second order may amount to ten or

twelve. The medullary investment and the sheath of Schwann accompany the nerves up to the very point of their attachment to the muscular fibre, but here the medullary sheath terminates abruptly, and without marked attenuation. In profile views no kind of distinction is to be perceived

Fig. 54.

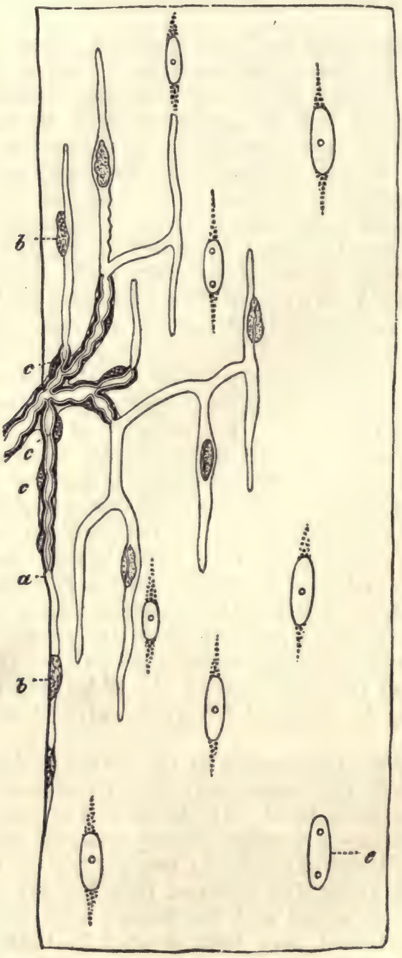

Fig. 54. Motor nerve terminations from the Frog. To avoid confusion, the transverse striæ of the muscular fibres are not indicated. At *a*, the passage of the nerve through the sarcolemma is seen in profile. The remaining portion of the intra-muscular cylinder axis expansion is more or less out of focus; *b b*, terminal nerve-bulbs; *c c c*, nuclei of the sheath of Schwann; *e*, nuclei of the muscle.

between the contour of the sarcolemma and that of the membranous sheath; indeed, the flat and granulated nuclei of the latter cannot unfrequently be followed into that part which all would acknowledge to be true sarcolemma, and which, as is well known, is in the frog destitute of nuclei.

No better evidence than this can be offered in regard to the continuity of the two tubes. At the point where the terminal nerve branches are abruptly given off, no elevation occurs in the frog, and only very rarely, if the nerve has been forcibly stretched at the point where it appears to be most easily torn, does the medullary portion retract, so that a small empty funnel hangs over the border of the muscular fibre. Beneath the sarcolemma the nerves, now destitute of medullary sheaths, may be recognized in the form of small, moderately broad fibres, extending in a direction parallel to the muscular fibres, and often somewhat exceeding the breadth of the finest medullated branches. These fibres form a delicate pattern between the contractile substance and the sarcolemma, dividing and giving off branches of nearly equal breadth, from which again others course in a nearly parallel direction. The whole system which they form is usually three or four times longer than the transverse diameter of the muscular fibre. It never invests the whole circumference of the contractile substance, and the branches never penetrate far into the interior of it. There can be no question that we have here an intra-muscular branched expansion of the axis cylinder, and that it is the axial portion of the doubly contoured nerves which alone penetrates the sarcolemma, and forms beneath it a wide-meshed and in part fibrillated plexus. The fibres of the plexus appear to be in part round and partly flattened; they are very transparent, with delicate and for the most part smooth, though here and there finely serrated, contours.

Good instruments show with sufficient sharpness that the intra-muscular axis cylinders are not diffusely troubled or granular at their terminations. The actual extremity is always a distinctly rounded point. Here and there the axis cylinders are somewhat enlarged, and in such places small strongly granular corpuscles may usually be observed, the size of which is intermediate between those of the nuclei in the sheath of Schwann and the well-known muscle nuclei. They are pear-shaped, with the pointed extremity directed towards the end of the axis cylinder, and are found not only in the expanded portions of the latter, but occasionally in other parts, though always lying close to the axis cylinder. The finer structure of these *terminal nerve bulbs* may be well seen even with ordinary microscopic powers, but still better with a very strong objective and a low ocular. A fine tortuous fibre may then be observed to separate from the axis cylinder, which in some places attains a considerable length, and, running along the bulb, terminates at its pointed end in a small swelling. This is all that has been ascertained up to the present time respecting the termination of the nerves in the Amphibia; the muscles of Tritons, Toads, the Proteus, and Salamanders presenting the same characters as those of the Frog. In these animals none of the granular and nucleated matrix is to be found which exists in the muscles of Arthropoda. A muscle nucleus with a small amount of protoplasm around it may, indeed, lie near the intra-muscular axis cylinder, but we never find at this point any special or peculiar disposition of this portion of the muscular contents. As regards the position of the terminal bulbs, as from their form these structures are named, they appear either to lie close to the nerves and on the same plane, or, as in the majority of instances, upon the latter and between them and the sarcolemma. Occasionally the author believes he has observed them to be absent. No physiological or morphological explanation has been advanced in respect to the significance of the nerve-bulb; but it appears highly probable that the nuclei represent the earlier formative cells of the nerve and muscle, and consequently may be compared in some measure in their structure to the nuclei of the cells connected with nerves in the cutis

of the tadpole that have been described by Hensen. According to this observer, the embryonic nerve fibres terminate in the nucleoli of these nucleated cells; the small pear-shaped knob at the end of the central fibre in the nerve bulbs would therefore correspond to the nucleoli.

Although there can be thus no doubt that in the Amphibia the nerve sheath is continuous with the sarcolemma, from whence it obviously follows that the contents of the former, if it extend beyond this point, must lie beneath the sarcolemma; yet this doctrine has received much opposition. The accuracy of the statements that have here been made may, however, be irrefragably proved by careful inquiry. The whole contents of the freshly isolated muscular fibre can be rendered fluid by hydrochloric acid of 1 per cent., whilst not only the primarily coagulated muscle plasma, but also the greater part of the muscle prisms, can be converted into a solution of syntonine. The entire contents of the muscle then, as is well known, move easily hither and thither in the sarcolemma, if care be taken that the lumen of the latter remains open, and all pressure be avoided.

The intra-muscular axis cylinders of muscular fibres thus treated dissolve first at the points, then separate along their whole extent from the sarcolemma, and fall towards the centre of the tube, so that on shaking they float to and fro in the fluid. And there is yet another experiment which has led Cohnheim to the same result. He dipped fresh muscular fibres for a short time in acid, treated them with a weak solution of nitrate of silver, washed them with water, and allowed them to blacken in the light. A fine precipitate of silver occurred in the form of thin membranes between the muscle cylinder and the sarcolemma, which, after exposure to light, surrounded the muscular substance with a black layer beneath the sarcolemma. In this layer, stained with silver, the whole intra-muscular nervous apparatus appears as a white silhouette, indicating that something is here intercalated between the sarcolemma and the contractile substance, and this indeed is the intra-muscular axis cylinder. This experiment is interesting on several other accounts; for, in the first place, previous to the blackening taking place, the form of the nerve termination appears with surprising clearness, because the fine layer, composed of the silver precipitate, surrounds in the first instance everything that is of nervous nature with very distinct limiting lines; and, secondly, a means is obtained which is unfortunately the only one at present known, by which preparations of muscles exhibiting the mode of terminations of the nerves can, for a few months at least, be preserved. Lastly, it shows that there is present between the sarcolemma and the axis cylinder on the one hand, and between this and the contractile substance on the other, a capillary layer not capable of precipitation with a silver solution under the conditions which the experiment accidentally realizes, a something which is different from that which surrounds the whole contractile substance beneath the sarcolemma. The experiment of making the nerves float by treating the muscular tubes with diluted hydrochloric acid renders the former indeed probable; for it is then seen that the axis cylinder, beginning at the point, only gradually separates from the sarcolemma, to which it appears to be very firmly adherent; the second method must at the same time appear still more important, because it indicates a more intimate connection between nerve and contractile substance than between this and the sarcolemma.

As regards the methods of investigation, it may here be added, that the greatest possible delicacy in manipulation is required, for the subject is one of the most difficult in the whole range of microscopic art, and is one also on which histologists are not, as yet, by any means unanimous, as

the short historical sketch at the end of this article sufficiently shows. It is not sufficient to take the muscular fibre from still living and contractile muscles, but care must also be taken that, whilst still under the scrutiny of the observer, they retain their contractility, the covering glass being prevented by supports from exercising any pressure upon them. Fibres affected with rigor mortis are totally unserviceable, and also those which have had their axes rotated, or which have been in any way damaged. Maceration in acids that are at all concentrated leaves no vestige of the intra-muscular nerves beyond a few interrupted and broken striæ. Extremely dilute acids, as acetic acid of 0·5 per cent., or hydrochloric acid of 0·1 per cent., do not, indeed, render the image any clearer, but they do not destroy it; the terminal bulbs, however, soften under their influence in quite a peculiar manner, breaking up into a brush-like set of fibres; a change that stands in strong contrast to the well-known shrinking of the muscle nuclei and of the sheath of Schwann, and most distinctly proves the difference of the corpuscles of the axis cylinder from those structures.

The mode of termination of the nerves in Fishes has been hitherto but little investigated; by the application of some of the methods already adopted for the muscles of Amphibia, however, evidence has been obtained that here also the nerves penetrate the sarcolemma, and, at the point of entrance, lose their medullary sheath. The few extended investigations which have been instituted upon the mode of termination of the nerves in the Torpedo ocellata will be mentioned in the following paragraph.

B. *Reptiles*, *Birds*, *Mammals*.—In these animals also the mode of isolating the fibres by means of Budge's solution permits the intimate union of the nerves with the muscular fibres to be proved; for, if the vascular network which contains the acid mixture have been removed with a brush, a short and frequently divided nerve stump often remains obstinately adherent to the fibre. An investigation by Rouget first led to exact conclusions in regard to the mode of termination of the nerves; since it demonstrated the existence of the Doyèrian eminence, in the first instance in lizards, and subsequently in warm-blooded animals. Rouget corroborated the statement he had already made, of the passage of the nerve through the sarcolemma, of the fusion of this with the sheath of Schwann, and added the important observation from his investigation of fresh muscle, such as can easily be obtained from Reptiles, that just beneath the point of entrance of the nerve, a mass of nuclei and granular substance, constituting a Doyèrian eminence, may be found exactly similar to that found in Arthropoda. And thus, although in the muscles of these animals there exists no such abundance of nucleated and protoplasmic formative material as in Arthropoda, yet this material is accumulated in greatest quantity immediately beneath the ends of the nerves. According to Rouget, the grumous mass, with the nuclei imbedded in it, constitutes the proper termination of the nerves, with which the axis cylinder becomes continuous, and thus modified, rests with a circular or elliptical flat basis on the contractile substance, the cylindrical mass of which it embraces for a certain distance, but never entirely surrounds. The rows of nuclei and of granular material that in Arthropoda extend for some distance along the muscle, are entirely absent in lizards and the warm-blooded vertebrates. The observation of Rouget soon received confirmation, and Krause appears to have been the first who correctly described and represented the nuclei of the nerve eminence, stating them to appear in the fresh muscle as small delicately contoured vesicles, with relatively large nucleoli; whilst, after the death of the muscle, and the addition of even

very dilute acids, they become wrinkled and filled with granules. Rouget had only seen, and at a later period depicted them, when thus altered. The nuclei which are seen at the extremity of the nerve are, moreover, not all alike; one portion belonging to the eminence, and another to the membrane which covers it; the latter being considerably smaller and flatter, rarely exhibiting a distinct nucleolus, and being always finely punctated or granular. As Krause has shown, they lie in the membrane, and may be regarded as the nuclei of the sheath of Schwann, where the latter, expanded over the eminence, is about to pass into the sarcolemma.

Nuclei presenting these characters are consequently only found upon the upper part of the eminence, so that their position alone renders it impossible to mistake them for the vesicular nuclei which are present only at the base of the eminence, or that portion of it which is directed towards the muscle. The small, hazy nuclei are distributed in far smaller number and irregularly in the membrane of the eminence, whilst the vesicular nuclei are arranged more or less definitely around the margin of the base. Finally, these small ellipsoids are placed with their long axis radially to the axis of the muscular fibre. They vary but slightly in size; in the lizards they are very little larger than the muscle nuclei, from which they are distinguished by their somewhat less elongated form, and by their presenting more rarely two nucleoli in their interior. In the warm-blooded animals, on the other hand, their size considerably exceeds that of the muscle nuclei.

The form of the nerve eminence in the muscles of Reptilia presents all conceivable varieties, being sometimes higher, and sometimes lower; sometimes having a long, elliptical, or even very extended basis; at others being nearly circular, or presenting the shape of a parallelogram with rounded angles. Those that are the most elongated are always the least prominent, forming, when the nerve end is seen in profile, scarcely any projection from the muscular fibre. In the warm-blooded animals, in which the nerve eminence is nearly circular, the eminence is likewise very flat,—relations which are here only alluded to, since they appear to be of subordinate importance.

The muscles of warm-blooded animals, as is well known, alter with great rapidity after death, and it is not surprising, therefore, that organs so delicate as the extremities of the nerves should likewise undergo cadaveric changes. Researches on the minute anatomy of these parts ought therefore to be commenced on Reptiles, whose muscles, especially at a low temperature, remain, like those of Amphibia, excitable for an astonishingly long period. It is, in truth, not difficult to recognize in lizards, as in Lacerta agilis and L. viridis, the mode in which the nerve terminates in the Doyèrian eminence. The granular mass, together with its nuclei, forms only the base or floor of the nerve end, whilst this is itself composed of a transparent non-granular plate, the *terminal nerve plate*, or the *motor nerve plate*.

At whatever period after death the muscles may be examined, there will always be found a third element in addition to those above named; namely, vesicles of various form, which are clear and transparent, pale contoured, and free from nucleoli; and these are to be found also in the nerve eminences of the warm-blooded animals. They are products of the very easily alterable nerve plate, probably acted on by the *post-mortem* formation of acid in the muscle.

Completely isolated muscular fibres removed from the still irritable thigh of a lizard, show characters which are almost precisely similar to those of the

frog; for though the muscular fibres are thicker, the nerve fasciculi are quite as much branched and divided. It is a matter of no difficulty, moreover, to find branches so placed that the point of entrance may be seen in profile; so that here also, from observations made on the perfectly fresh and living object, no doubt can exist in regard to the relations that exist between the nerve and muscle. The nerve plates can, on the other hand, be better surveyed and examined in face, enabling the nuclei to be well seen. A structure of beautiful form appears between these in pale bands, consisting of a

Fig. 55.

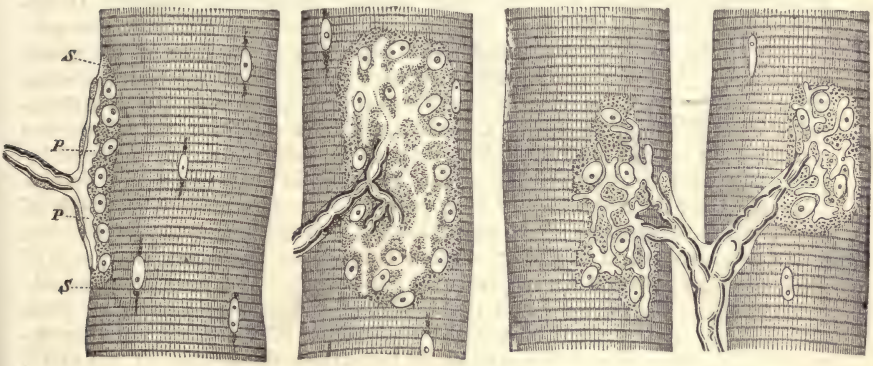

Fig. 55. Muscular fibres with nerve ends, from Lacerta viridis.

A. Seen in profile; *p p*, the terminal nerve plate; *s s*, the base or support of the plate, consisting of a granular mass with nuclei.

B. The same as seen in a perfectly fresh muscular fibre, whose nerve ends are still probably excitable; the delicate and pale contours which the frequently branched plate naturally possesses are not expressed in the woodcut.

C. The same as it appears after the death of the nerve end, as, for instance, two hours after poisoning with large doses of woorara.

delicate pattern of parallel lines, which sometimes form longer cords, sometimes sinuous plates, which are again perforated. If the muscle be tetanically contracted, the plates appear folded like the crop of a bird, their softly sinuous edges being angular and serrated. There may also be found at the periphery small delicate processes with club-like ends. Careful focussing with the microscope, with a profile view, shows that the terminal plate lies immediately beneath the membrane of the nerve eminence, and just above the granular mass; for it will be found that the greater number of bright nuclei first make their appearance on effecting the adjustment for depth. A few of the latter do, however, lie on the same plane as particular parts of the plate, where, for instance, they, with the granular mass surrounding them, occupy cavities in, or lie between, its folded borders. The above-described image is extraordinarily pale and delicate, and only a practised eye can recognize it in quite fresh and still contracting muscle. It is seen, for example, in the very thin cuticular muscles of the Coluber matrix, which can be placed under the microscope without preparation, and which present a few nerve ends supplying some of the fibres on their surface. Now inasmuch as these muscles contract through their whole extent when their nerves are irritated, and whilst still under observation, we may conclude with cer-

tainty that the pale and delicate image of the terminal plate represents truly the living condition, not only of the muscle, but of the nerve, whose termination it forms.

In those cases where the muscular fibre dies whilst in a state of rest, this image becomes continually clearer and sharper; whilst the contour of the plate, in the first instance, simply becomes more clearly defined, without undergoing any essential change of form. But since portions of muscle thus excised rarely die in the condition of physiological rest, but become tetanically contracted before the occurrence of rigor mortis, and are then fixed in this condition by coagulation, it is comparatively rare to meet with the earliest stage in which the image is best shown. It is advantageous, therefore, to permit the muscles to die out in the dead body, and to examine them before they are so much stiffened as to become cloudy and opaque. It appears, therefore, that the most distinct definition of the plates occurs previously to the death of the muscle, and especially at the time of the death of the nerve in the stage known to physiologists as that in which the muscle can no longer be excited to contract through the nerves, but is still capable of responding to direct stimulation. This condition, in which the muscle long retains its irritability, may, as is well known, be induced by poisoning with woorara, if the poison be given in large quantities, and be allowed to act for a sufficiently long period to produce evident paralysis of the terminal extremities of the motor nerves. Muscles that have thus been poisoned present in a distinctly marked manner an increased sharpness of contour of the terminal nerve plate—an appearance which may consequently be regarded as the outward and visible sign of commencing paralysis. This may perhaps be the result of a slight contraction of the plate, or of an inappreciable retraction of the granulated basis from the borders of the plate, which is nevertheless sufficient to induce the alteration in the image that we observe.

In the perfectly stiffened muscle, when its reaction has become acid, the contours of the plates change their form; the terminal nerve organ becoming continuously more and more folded and notched, and at length divided off into spherical masses, vesicles, or other forms, which are sometimes most remarkable. The whole of these changes may also be quickly induced by the action of very dilute acids; so that, in point of fact, no difference is observable from the ordinary cadaveric appearances, especially if, in order to dilute the acids, serum instead of water be employed, which prevents imbibition from taking place. This is, perhaps, a proof that the later cadaveric changes of the terminal plate of the nerve depend on the *post-mortem* acidification of the muscle.

What has been already stated in reference to the muscles of Lizards and Snakes is equally applicable to those of warm-blooded animals, and also to those of Man. It is, indeed, scarcely possible to break up human muscles under the microscope in so fresh a condition that they may still be excited by irritation of their nerves, but they may be obtained so well preserved from amputated limbs that the terminal plate can be demonstrated with its nerve eminence but little altered, or, at all events, not separated into distinct masses by a process of constriction. The plates can be immediately seen in the muscles of Mammals and Birds, only these should be prevented from becoming too rapidly stiffened; and this may easily be accomplished by lowering the temperature of the preparation to 32° Fahr., and the addition of serum at the same temperature on cooled slides. With the rigidity which here always supervenes on the tetanic condition, the object ceases to be available for investigation, chiefly on account of the deeper-lying fibres

of the muscle becoming too opaque; and as the terminations of the motor nerves in these animals become paralyzed instantaneously after the cessation of the circulation of the blood through them, it follows that, even in the freshest condition of preparations taken from warm-blooded animals, the plates do not present very sharp outlines.

The determination of the thickness of the terminal plate and its relations to the adjoining parts, are points that demand methodical investigation. In the small nerve eminences of slender muscular fibres it presents itself when examined in profile as a thin mass projecting externally into the medullated nerve fibre somewhat in the form of a cone, with a sinuous inferior border, which is turned towards the basal substance or matrix on which it rests throughout its whole extent, and by which, as by a layer equal to itself in thickness, it is separated from the contractile substance. In accurately made transverse sections of the frozen muscles of Lizards, it appears, on the other hand, in the form of an irregularly reniform mass which, at some points at least, gives the impression of being directly superimposed upon the muscular prisms. Such preparations remove every doubt respecting the relative position of the contractile substance, the granular substance of the nerve eminence, the nerve plates, and the sarcolemma, which undoubtedly lie in that order from within outwards. Moreover, transverse sections of frozen muscles with their nerve eminences afford an insight into the thickness of the nerve plates. They show that this, as a whole, is not inconsiderable; that in the central part it is nearly as large as the short diameter of a nucleus of the basis substance, though at the edges and irregular processes it is far smaller; so that were it not for their transparency the transverse sections of these parts might be mistaken for granules of the basis.

Preparations made with osmic acid stain the nerves as far as the apex of the nerve eminence of a bluish black color, whilst the contractile substance, the nerve plate, and the basis substance assume a clear yellow tint, and fat molecules in the muscle become brown,—reactions which prove that the whole intra-muscular nerve termination loses the characteristic constituents of the nerve medulla. The terminal nerve plate can be brought into view in an isolated condition, though certainly not situated externally to the muscle, without other addition than clear muscle serum. Isolated muscular fibres from the lizard, fixed under a covering glass, frequently exhibit, when they are in a complete state of rigor mortis, such contractions of the muscle coagulum, that large balls of this material accumulate in swollen portions of the sarcolemma, between other smaller spaces, filled only with muscle serum. If the last mentioned empty spaces happen to occur at the place of the nerve entrance, the plate hangs free in the lumen of the sarcolemma, and it is deserving of notice that it even then still adheres to the protoplasmic substance and nuclei which constitute the basal substance of the nerve eminence. It appears, therefore, that further investigation is requisite to enable a positive statement to be made in regard to the union that exists between the two constituents of the nerve eminence.

From what has been now advanced, we may conclude, then, that the appearances presented by the extremities of the motor nerves are so various that scarcely any scheme can at present be constructed that shall give a representation, the morphological and physiological features of which shall be applicable to all animals. According to Doyère, the pale, transparent, and non-granular nerve of Milnesium tardigradum becomes converted at the periphery into a finely granular eminence, which partly surrounds the equally pale, untroubled, and non-striated muscular fibre, and may extend a

little distance along its border. These statements have been completely corroborated by renewed and very careful investigation of the Tardigrada (bear animalcules) by V. Greeff. This observer readily found the appearances so long known from Doyère's drawings, but also observed a small spherical nucleus to be constantly present in the little nerve eminence, with a few sparsely scattered somewhat larger nuclei, very sparingly surrounded by punctated protoplasm, adherent to the muscle, and which for the most part lie at a considerable distance from the termination of the nerve. V.

Fig. 56.

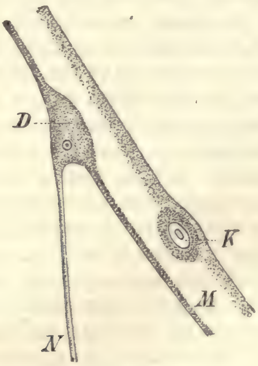

Fig. 56. Termination of a nerve in Milnesium tardigradum (one of the sloth or bear animalcules), according to Greeff. M, muscular fibre; K, nucleus of muscle; D, eminence of Doèyre; N, nerve.

Greeff was unable to find, either on the nerve or on the muscle, anything corresponding to the sheath of Schwann or to the sarcolemma.

Of those points which have been described by a few observers in respect to the termination of the nerves in the non-striated muscles of the lower animals, and in the smooth muscular tissue of the Vertebrata, mention has already been made under their appropriate heading. Trinchese has given some details respecting the termination of the nerves in the muscles, that have hitherto been regarded as unstriated, of Helix pomatia and of Bowerbankia. According to him, a fine nerve fibril enters the large muscular fibre cells of the muscular apparatus of the foot of Helix pomatia near their centre, divides immediately in their interior into two branches, which extend to the two pointed ends of the muscular fibre in the form of two elongated, and towards their extremities spirally twisted, threads. In the centre, and just subjacent to the point of division, an ellipsoidal accumulation of finely granular substance exists. In Bowerbankia, whose muscles Trinchese likewise describes as smooth bands, only a low conical process of the somewhat broader nerve fibre is present, in which cone, and at its base where it touches the muscle, is the granular material with a spherical nucleus and nucleoli.

The question now arises, what is the essential nature of the termination of the motor nerve? The author cannot doubt that this is at present most imperfectly known in the Arthropoda. Rouget, indeed, states that he succeeded in perceiving a prolongation of the axis cylinder in the nerve eminence in the form of a system of branched fibres; and we must probably admit that this system does exist: but the further statement of Rouget,

who attributes nervous properties to this part alone, as was generally previously admitted in Germany, and that this ramified system of fibres lies beneath the nucleated substratum, appears to the author to be very much in need of confirmation. Engelmann, who also examined the muscles of the Arthropoda, depicted a transparent homogeneous and quite vesicular mass at the apex of his nerve eminence, which appears to be the analogue of the terminal nerve plate found in Reptiles and Mammals, and, like these, to be bounded throughout the greater part of the surface turned towards the contractile substance by a granulated substratum. If this supposition be established—namely, that in the Arthropoda also a non-granular plate, or even a structure similar to the intra-muscular axis-cylinder system of the Amphibia is present, covering the granular nucleated substratum, to which Rouget's statements appear to point—we should have obtained the much-desired uniformity of structure; and there would then be *one* mode of nerve termination, in which the nerve ends with a motor plate in a nerve eminence, resting on a nucleated bed of protoplasm or a matrix; and a *second* mode, in which, as in Amphibia, the matrix is absent, and the nerve ends in an elongated and branched fibre-like plate. Only the Amphibia possess terminal bulbs, the analogue of which Cohnheim stands alone in considering to be found in the plates of Lizards; that is to say, in the small granular sessile and more conical corpuscles that are found in these animals, respecting which further investigations are needed. Greeff first advanced the view that the mode of nerve termination in Milnesium may be assimilated to an expanded flat ganglion cell adherent to the muscular fibre; and were we to transfer this idea to the higher animals we should have to regard their nerves as terminating in a collection of ganglion cells, corresponding in number to the nuclei present, or in a ganglion cell containing many nuclei, or perhaps in a series of ganglion cells which have become fused together; that is to say, which have formed a ganglionic nerve plate. This view does not, however, materially advance our knowledge; for, even if it be correct, we shall have to seek for the minute anatomy of these terminal ganglion cells just as has been done for those of the nervous centres and others; and if we have already acquired a considerable amount of information respecting these, we yet know still more in regard to the nerves terminating in muscle, since we are acquainted with the plates, and their subjacent protoplasm, from which they are rarely sharply differentiated. We need not despair of discovering their analogue in all nerve eminences, even in the minute ones of Milnesium, though perhaps better instruments and improved methods of investigation will be required to discover the finer points of their structure than those we at present possess.

As long as the granular contents of the nerve eminence were regarded as the proper continuation of the axis cylinder, as it now is by Rouget, in the case of Mammals and Reptiles—though he does not perceive that this involves a contradiction to his former very decisive and explicit statements that in the Arthropoda his system of fibres was the only part of a truly nervous nature, the remaining structures, *i. e.* the granular mass and the nuclei, being accessory—so long could the view be maintained that the nerve becomes directly continuous with the contractile substance. This last idea is, however, opposed, from a morphological point of view, by a consideration of the mode of nerve termination in the frog; since, if there be a fact in the whole range of this inquiry capable of being easily ascertained, it is the invariably sharply defined and distinct termination of the intra-muscular axis cylinder in the Amphibia. That view is also, and has long been, opposed by physiological considerations; for it is demonstrable

that the muscle does not act upon the nerve fibre, but that, on the contrary, all stimuli are conducted from the nerve to the muscle, and never in the inverse direction; and for this purpose the nerve termination forms, as we now know, the visible structure. It may indeed be that a finer series of radiating processes from the nerve plate may penetrate between the granules of the substratum than we are at present disposed to admit; and many circumstances may be adduced in favor of this supposition, as, for example, the intimate adhesion of the two parts to one another, even when the contents of the eminence no longer rest upon the muscle. It is obvious, then, that it remains to be shown that the substratum constitutes a direct transition to the contractile, since there are muscles, especially amongst the Amphibia, in which this structural characteristic is entirely absent.

The present state of our information upon these points may be shortly expressed as follows:—

In all transversely striated muscles the nerves terminate beneath the sarcolemma, the sheath of Schwann becoming continuous with the latter. Up to this point the axis cylinder is accompanied by the medullary sheath. The extremity of the axis cylinder always corresponds to a remarkably broad expansion, which constantly forms a flat branching mass. This terminal nerve plate sometimes presents the character of a membrane, and at others resembles a system of fibres. In the greater number of cases the plate rests upon a substratum of nuclei and finely granular protoplasm, whilst in others this material is absent, and the nerve plates possess the so-called terminal nerve bulbs. The extremity of the nerve never penetrates into the interior of the contractile cylinder, and, on the other hand, never entirely invests it. Short muscular fibres usually receive only one nerve; but long fibres have several.

We may add, hypothetically, that the substratum represents the remains of a formative material important in the development of both the muscular and nervous tissue, and that a similar explanation may be offered of the nature of the terminal nerve bulbs in respect to the nervous tissue.

History and Literature.—The preceding observations have been so ordered as to give the historical development of the principal facts with which we are at present acquainted respecting the modes in which nerves terminate in muscle. Those observers, therefore, that have contributed any essentially new information on the subject, have already been mentioned. A few remarks may, however, still be added, since the questions involved have given occasion to lively controversy during the last ten years.

In few departments of histology has methodically prosecuted investigation, proceeding always from hypothesis, proved more fruitful in results than in relation to the question of the connection existing between nerve and muscle. The modern science of morphology has undoubtedly reaped the value of that experience that has been obtained in all other branches of knowledge, in having become a special subject; and the example before us will serve, perhaps, to point out the advantages that histology, which inclines as much towards morphology as towards physiology, has to anticipate from hypotheses borrowed from both departments.

We shall here leave unnoticed the older works, so far, at least, as they bear upon the unsatisfactory view of nerve loops.

In the same year that Savi (2) communicated his important observations of the division of the primitive nerve fibres in the electric organs of the Torpedo to a scientific congress at Florence, Doyère (1) discovered the termination of the motor nerves in Milnesium tardigradum. Remak (3) then incidentally stated that in mammals the nerves appeared to him to end in a plexus of pale fibres, winding around the external surface of the sarcolemma. Quatrefages (4) verified the discovery of Doyère in the case of Eolidina. In 1844, E. Brücke and Joh. Müller first observed the division of primitive nerve fibres in the muscles of the eye of the pike, and R. Wagner (6) observed the same thing in the musculus hyoideus of the frog. Kölliker (7) soon after established the Doyèrian mode of termination of the nerves in the larva of Chirono-

mus, and Reichert (8) demonstrated the division in the cutaneous muscle of the thorax in the frog, where he found by direct counting that a few nerve fibres furnish more branches than the number of the muscular fibres to be supplied. The Doyèrian mode of termination was again corroborated by Meissner (9), in Mermis and Ascaris, and by Wedl (10), Walther (11), and Munk (12), in several Nematodes. At a somewhat later period, Schaafhausen expressed himself in terms similar to those of Remak, and believed that he had seen a fine network of fibres, tinted with carmine, investing the whole muscular fibre. At this date the above-described mode of termination of the nerves in the muscles of insects was discovered (14, 15), and inasmuch as the nerves were here proved to terminate beneath the sarcolemma in muscles possessing this membrane, the view entertained by Schaafhausen respecting the similarly constructed muscles of vertebrate animals was rendered improbable. Nevertheless, a similar conclusion was arrived at by Beale (16, 17), an energetic inquirer who maintained that in the frog in particular the nerves gave off relatively broad nucleated fibres. Since, however, he did not adopt the method of isolation, but colored his preparations deeply with carmine, it is possible he may have been deceived by the confusion of fibres traversing the accessory structures associated with muscle. Investigations undertaken upon isolated muscular fibres from the frog (18, 20) now led to the discovery of the intra-muscular axis cylinder and its terminal bulbs. The penetration of the nerve through the sarcolemma, now for the first time demonstrated, was established by Margo (19), who considered the axis cylinder terminated in a system of nucleated and granulated fibres which penetrated the contractile substance to all depths. The views of Margo, which he subsequently extended to the Arthropoda (27), have never found adherents, since they clearly rested on illusory appearances caused by the well-known serially arranged interstitial granules which are present in so many muscles. In the mean while Kölliker reverted to the views of Beale, but with the addition that he regarded the nerves as frequently exhibiting free extremities, and did not, as Beale thought, form a completely closed plexus. Resting on this assumption, Kölliker, who undoubtedly first rediscovered the intra-muscular axis cylinder of the frog (25, 26), maintained that the terminal bulbs there seen were really nuclei of the sheath of Schwann. Krause (24) and Rouget (29) agreed with him in all points, and now, whilst Beale (28) retained his first opinion as being applicable to all classes of animals, Rouget (29) came forward with his discovery of the nerve eminence in reptiles and warm-blooded animals, and was corroborated in all essential particulars by Krause (31), Engelmann (34, 38), and the author (39, 40) ; by the latter, indeed, with special emphasis, because Krause had given quite a different signification to the nerve eminence ; had placed it external to the sarcolemma ; had described the nuclei as being situated in the membrane, and the whole structure as being an organ more analogous to the nerve bulbs invested by the sac-like sheath of the nerve. The opposite views that Krause took on these points to the descriptions given by Rouget, Waldeyer (35), Letzerich (37), and Engelmann, were based on the application of uncertain methods of investigation, especially in the attempt to establish the presence of a sharply defined line belonging to the sarcolemma between the contractile substance and the substratum of the nerve plate, which he obtained by the coagulation of the muscle in bichromate of potash, or by the examination of the transverse sections of dried muscle. The lines thus produced do, indeed, lie subjacent to the sarcolemma. It is conceivable that Krause, and perhaps also Letzerich, if the author rightly comprehends the latter, perceived in the nerve eminence the first indications of the nerve plate ; that which Krause described as a pale terminal fibre ending in a bulb being a portion or an optical longitudinal section of the nerve plate, whilst that which Letzerich compared to fluid wax was the plate itself. Thus, in the first investigation on the muscles of Reptiles in Germany, the nerve plate was recognized (47) as the immediate and proper terminal organ of the axis cylinder, whilst it was at the same time established that the granulated and nucleated mass previously taken for it was only the substratum of the plate. That which Rouget, Engelmann, Waldeyer, and Krause regarded as the nerve plate, advantageously exchanged its name for that of nerve eminence (Doyère's cone), in order to preserve the otherwise very appropriate term of *terminal plate* for the true extremity of the nerve, which expresses well the peculiar form that it presents. The nerve plate was soon recognized as an essential constituent of the nerve eminence in the muscles of warm-blooded animals and of man (48). In the mean time Rouget (43) and Krause (41), in the case of the frog, pursuing the method suggested by Waldeyer, who also believed he had seen a nerve eminence in that animal, adopted another view, Krause describing in the muscles of the frog extremely minute nerve eminences which he believed to be situated externally to the sarcolemma, and to which long, pale, and delicate nerve fibres ran, whilst Rouget considered that the nerves ended by a blunt extremity at

the sarcolemma, which was itself continuous with the sheath of Schwann. Neither a nerve eminence, nor any similar prolongation of the axis cylinder is present, according to Rouget, in the muscles of the frog. The true intra-muscular termination of the nerve again apparently escaped the observation of both observers; for Krause, in preparations where the nerves had undergone much stretching, and had on that account become attenuated, mistook the point of attachment of the nerve which had thus been rendered conical with the ultimate nuclei of the sheath of Schwann for the nerve eminence; whilst Rouget obviously overlooked the entire expansion of the now no longer medullated nerve, after he had been accustomed to the infinitely more sharply defined images of the same parts in the muscles of lizards. In the mean while Engelmann (38) had been successful in discovering the elongated expansion of the axis cylinder in the frog, with the exception only that he denied the minute anatomy of the terminal bulbs, and believed a granular substratum to be here present, constituting an intermediate structure between nervous and contractile tissue, and continuous with both. The objections to this view, extended by Engelmann to the muscles of all animals, have been already adduced, and it need here only be added that his description of the granular mass in the frog is decidedly erroneous. The most satisfactory demonstration of the accuracy of the mode of termination of the nerves described in the text results from the application of the silver mode of preparation, and has been furnished by Cohnheim (46, 60); this mode is equally well adapted to display the terminal nerve plate in the Doyèrian eminence which comes into view in muscles blackened with silver, in the form of a beautiful white pattern. The same author has pointed out that the isolation of the nerves from the remains of the nerve eminence adherent to them, accomplished by Krause with the aid of moderately strong hydrochloric acid, is not to be regarded as a proof of the eminence being situated on the outer surface of the sarcolemma, because the acid under the conditions maintained by Krause, to wit, degree of concentration and duration of action, effects the solution of the sarcolemma, and consequently lays bare the muscle, and breaks down the continuity of the nerve with the muscular fibre. The existence of the terminal plate has still more recently been vigorously contested by Rouget (56) and Krause, who explain the whole appearance as a hitherto undescribed *post-mortem* phenomenon of coagulation, in contradiction to which, again, Rouget stated that the true termination of the axis cylinder in the nerve eminence consists in its metamorphosis into a granular mass with interspersed nuclei. Rouget soon again retracted this view for the muscles of Arthropoda, and especially for those of Crustacea, in which he discoved an analogue to the plate, or at least to the more fibrous mode of the termination of nerve fibres that occurs in the frog. It is reserved for further research to decide whether Rouget's statements are correct, to the effect that this fibre system, in opposition to all analogy derived from the Vertebrata, penetrates the granulated substratum, and comes into direct contact with the contractile substance. Engelmann's observations (67), at all events, expressly establish the latter point.

To all appearance, the general results of inquiry upon the important question of the mode of termination of the motor nerves seem to show that the views of Remak, Beale, and Kölliker must generally be given up, whilst Rouget admits that in the case of Crustacea, at least, the axis cylinder does not terminate in a band-like and granular manner. It appears, lastly, from the very recent brief essay of Krause (64), that this author also has given up his two former views in respect to the muscles of Amphibia, and has now actually seen the fibre system of the intra-muscular axis cylinder, and also, by the application of the coloring method with solutions of gold, the exceedingly beautiful form of the nerve plate in the muscles of Lizards. The next step that has now to be taken in advance, is to interpret the relations of the lower surface of the plate to the granulated substratum. The author is unable to express an opinion upon the statements of Trinchese (63), which relate to the nerve eminence of the Torpedo. According to this observer, the nerves of this fish possess duplicate sheaths at their extremity, of which only the perineurium is continuous with the sarcolemma, whilst the nucleated sheath of Schwann accompanies the axis cylinder where it penetrates into the nerve eminence, and everywhere loosely invests the flat plexus formed by the division of the axis cylinder. Trinchese describes peculiar ganglionic enlargements on the thus modified axis cylinder, and true terminal ganglion cells, with nucleus and nucleoli, on the projecting extremities of the network; other nuclei distributed through the nerve eminence he refers to the sheath of Schwann contained in the muscle. The drawings of Trinchese, although taken from preparations materially modified by diluted hydrochloric acid, and undoubtedly deprived of their best qualities, show what excellent materials were at his disposal, and render it extremely probable that these animals present the most magnificent motor terminal plates in existence, though the delicacy and beauty of their form are lost in all but physiologically fresh specimens.

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CHAPTER VI.

THE BEHAVIOR OF MUSCULAR FIBRES WHEN EXAMINED BY POLARIZED LIGHT.

By E. BRÜCKE.

When muscular fibres are examined with a microscope to which a polarizing apparatus is attached, remarkable and instructive phenomena are observed. If the field be darkened by crossing the planes of polarization of the Nicol's prisms, those fibres only disappear which lie parallel to the plane of polarization of one or other of the prisms; the rest, which cut those planes at various angles between 0° and 90°, appear of a gray color upon a black ground, the most distinct being those which cut them at an angle of 45°. In those parts where the muscular fibres running parallel with one another are arranged in several layers, the color assumes a whitish tint, passing into yellow. The tint varies with the thickness of the layers, precisely as the succession of colors in Newton's rings, from the centre towards the circumference. If one of the Nicol's prisms be turned to the extent of 90°, so that the field becomes clear, and attains its maximum brightness, the complementary tints make their appearance. These phenomena, with others that will presently be described, are equally apparent when the muscular fibres are thoroughly impregnated with, and surrounded by, strongly refracting fluids, as glycerine, turpentine, and Canada balsam. This is essentially owing to the circumstance that the muscle substance is doubly refractile, two systems of undulations propagating themselves according to different laws, and interfering the one with the other.

This explanation had already been given in 1839 by Prof. C. Bœck,* of Christiania, who was the first that applied the polarizing microscope to the investigation of animal and vegetable tissues; and no other intelligible explanation has since this period been advanced of the phenomena observed.

The next question to determine is, whether the entire substance of the muscular fibres possesses an equal power of double refraction, or whether it it is possible to distinguish doubly refracting from isotropal parts. If sufficiently high magnifying powers are employed, and the observations be made on animals which have large sarcous elements, amongst which our large water-beetle, the Hydrophilus piceus, is the best, it will be immediately seen that only the sarcous elements are doubly refracting, and that the intervening material which separates them from one another is isotropal; for it remains dark in the dark field of the crossed Nicol's prisms, in whatever azimuth the muscular fibre to which it forms a part may be placed; it is just as dark in those muscular fibres which form an angle of 45° with the polarizing planes of the prisms, as in those which make an angle of 0° or of 90° with those planes.

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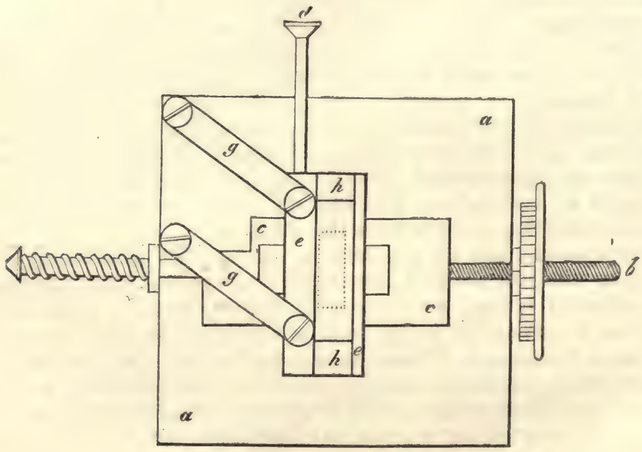
* *Transactions of the Scandinavian Society of Naturalists in Götheborg in* 1839, *and in Copenhagen in* 1840. *Report on the progress of Anatomy and Physiology in Scandinavian Literature in the years* 1840–1843, by Ad. Hannover, in J. Müller's *Archiv für Anatomie u. Physiologie*, 1844.

This becomes still more evident if a water-beetle be killed by immersion in strong alcohol, and after a few days' maceration the muscles of one of its thighs be placed in oil of turpentine, and finally in Canada balsam. Owing to the high refracting index of the balsam the muscular fibres appear in ordinary light very pale and transparent, and all the stronger shadows vanish; but on this very account all the phenomena caused by double refraction appear with corresponding distinctness under the polarizing microscope. But in what way are the sarcous elements doubly refractile? Are they positive or negative? Are they uniaxial or biaxial?

If a transverse section of the muscle hardened in spirit be thoroughly impregnated with Canada balsam, and examined with the polarizing apparatus, it will be found that as it is turned round the axis of the instrument a portion of the cut surface remains constantly dark in the dark field of the crossed Nicol's prism, while the remainder, in the effective azimuths—that is, in those in which they make angles between 0° and 45° with the planes of polarization—become clear. It soon appears that such as always remain dark are those which lie exactly parallel to the axis of the instrument, whilst this is not the case with the rest. There is thus an optic axis precisely corresponding with the longitudinal direction of the muscular fibres. Now, inasmuch as this coincides with the longitudinal dimensions of the straight prisms represented by the sarcous elements, and since we are unable

Fig. 57.



to discover a second optic axis, or any indication of its existence, we must regard the sarcous elements as uniaxial.

Are they positively or negatively doubly refractile? In order to determine this I have constructed the instrument shown in the accompanying figure. The blackened brass plate *a a*, perforated in the centre, and connected to the object plate of the microscope, possesses two slides, which can be moved over one another; the lower *c c* by means of the micrometer screw *b*, the upper *e e* with the unassisted hand by means of the handle *d* on the parallelogram *g g*. Both slides carry prisms of quartz, the upper one movable in the direction of its length in a groove *h h*; the lower one fixed, and only movable together with the slide by means of the micrometer screw The prisms rest upon their thin edges, and the stage is perforated immedi

ately beneath them, so that the light is freely transmitted. They have both a corresponding angle of 1° 6′ 54″, and are so cut that one of the inclined planes in each is parallel to the crystallographic principal axis, so placed that the light reflected from the mirror of the microscope passes perpendicularly to this axis in each, and so arranged that the two principal axes cross each other at right angles, each of them making an angle of 45° with the polarizing plane of the subjacent Nicol's prism. Since the two prisms act in a contrary sense, so that the ray which is ordinary in the first becomes extraordinary in the second, there are obtained, if the Nicol's prism situated above the ocular be made to cross that which lies below the quartz, a few black striæ, where equal thicknesses of the latter lie over one another, whilst on both sides colors appear in the sequence of the Newtonian system of rings for reflected light. The prisms, moreover, by sliding can be so arranged that the black stria which is present when the differences of velocity of the rays = 0, or the color corresponding to some determinate difference of the ray, can be made to occupy the middle of the field.

I now make the upper of the two quartz crystals an object stage, and distribute the muscular fibres of Hydrophilus piceus upon it in such a mode that, whilst some lie parallel to the principal axis, others are arranged perpendicularly to it. If the micrometer screw is now turned so that an increasingly thick portion of the lower prism is gradually brought into the field, it will be remarked that each color is first assumed by those muscular fibres which are arranged at right angles to the axis of the upper prism, then by the ground, and lastly by the muscular fibres which lie parallel to the axis of the upper prism. If the screw be turned in the opposite direction, these colors are first shown by those muscular fibres which lie parallel to the axis of the upper prism, then by the ground, and then by the fibres which stand perpendicularly to the axis of the upper prism. Every muscular fibre therefore acts optically like a thickening of the prism to the axis of which it is parallel, or, which is the same thing, as an attenuation of the prism to the axis of which it is perpendicular. The sarcous elements are consequently positive like rock crystal.

The proof of this is obvious. Since the light passes through the first prism at right angles to its principal axis, the plane of vibration of the extraordinary ray is perpendicular to the principal axis, that of the ordinary ray parallel to the principal axis, or at an azimuth of 90° from the former. The extraordinary ray precedes the ordinary, and interference phenomena exhibit differences of shade, which are dependent on the thickness of the prism, and the wave-lengths of the ordinary and extraordinary ray. The two rays emerge from the first prism with this difference of shade, and as they penetrate into the second, which crosses the first at 90°, the ordinary ray can only produce vibrations parallel to the axis, the extraordinary only those which are at right angles to the principal section. Thus the vibrations which constitute the ordinary rays of the first prism form the extraordinary in the second, and *vice versâ*. Since now in the second prism the extraordinary ray is propagated with as much increase of rapidity as in the first, it is clear that the difference of velocity must diminish until equal thicknesses of the two prisms are traversed; that it is then = 0; and if the passage through the second prism is longer than through the first, it increases with opposite signs.

If now a doubly refracting body be placed on the upper prism, the optic axis of which is parallel with the principal axis of the crystal, the ordinary ray of this upper prism will be propagated as an ordinary ray in it; and the extraordinary as an extraordinary ray. It acts thus upon the difference

of shade as a thickening, if the ordinary in it, as in the prism itself, is propagated less rapidly than the extraordinary; but if the opposite occur, it must operate in the same manner as a thinning of the prism with the principal axis of which its optic axis is parallel.

An important question still remains, which can be solved by the help of the polarizing microscope: Are the sarcous elements to be regarded as single and individual elementary bodies, or as groups of solid bodies capable of being variously disposed? If the muscles contract, the fibres are seen to become thicker, and the transverse striæ to approximate. Each sarcous element must consequently change its form, and come shorter and thicker. If such a change of form result from any force acting in an elementary solid body, the operation of that force must extend as far as the individual molecules, the optic constants must be changed, and it is not conceivable that they should be so changed that the ordinary and extraordinary ray, after they have traversed equal thicknesses in the same direction, should present again the same difference in velocity that they offered under similar circumstances before the change of form.

But it is quite a different matter if the sarcous elements are groups of solid doubly refracting bodies, of which each individual remains unchanged in form in the act of contraction. The form of the whole group—that is, of the sarcous element—is here changed by an alteration in the arrangement of the several corpuscles, just as in a company of soldiers groups of various breadths and depths are produced by changes in the position of the several individuals. In the latter case the optic constants are not altered in the act of contraction, and the rays on this account, if they have traversed equal thicknesses in the same direction, must constantly exhibit the same differences in velocity, whether the muscle be in the relaxed or in the contracted condition.

Since we have a measure of the difference of velocity in the colors which appear under the polarizing microscope, we are enabled to answer the question experimentally, whether the optic constants of the contractile substance change during contraction to any considerable extent or not. All the investigations I have directed to this point have had a negative result; *i.e.*, I have never seen any alteration of color that could not be entirely referred either to changes in the thickness of the layer traversed, or in the angle which the rays undergoing interference make with the optic axis. As, therefore, I have in vain sought after a change of the optic constants, I must maintain that the sarcous elements are not elementary and simple solid bodies, but groups of smaller doubly refractile bodies. These doubly refracting bodies I have called Disdiaclasts, after the phrase employed by Erasmus Bartholin, the discoverer of double refraction in calc spar, in the title to his well-known treatise.* The composite nature of the sarcous elements furnishes an explanation of the various appearances presented by muscles in a state of rigor mortis. In my researches on the structure of muscular fibres with polarized light,† I have constructed nine different schemes, and we may not unfrequently see one and the same muscular fibre in different parts representing two different schemata, which is attributable to the circumstance that, in the several sections of the fibre, the sarcous elements have divided with great regularity into smaller groups of disdiaclasts, so that much narrower systems of transverse striæ appear in these sections

* *Experimenta Crystalli Islandici Disdiaclastia quibus mira et insolita Refractio detegitur.* Havn, 1869.

† *Denkschriften der Wiener Akademie der Wissenschaften*, Band xv., *Separatauflage, Wien. bei Gerold.*

than in others, though they are neither shortened nor thickened by contraction.

Margo,* who found that the sarcous elements exist also in the fibres of the adductor muscle of bivalves, frequently saw the muscles in Anodonta only partially striated.† In this case the sarcous elements of the transversely striated parts lie next one another in regular rows; but in those parts that, with weak powers, appeared homogeneous, he found, with higher powers, instead of numerous small irregularly distributed granules, small groups of disdiaclasts.

If the living muscular fibres of frogs or beetles be immersed in water, they, as is well known, die rapidly; the ends swell up strongly, and the contractile contents ooze out of the sarcolemma. If such terminal portions of fibres be observed under the polarizing microscope, with the prisms crossed, no sarcous elements are observed in them, but they present the appearance of fine silvery-gray clouds distributed in the dark field. Here the sarcous elements have become disturbed, whilst the absorbed water has shifted the several disdiaclasts from their position. This state, resulting from the imbibition of water, is essentially different from that induced by the action of dilute acids, which effect a change in the substance of the disdiaclasts themselves, and take away their power of doubly refracting light. In conclusion, I will add a few remarks on the external and internal aids to the study of muscular fibres in polarized light.

To whomsoever the foregoing details and the ordinary works on physical science are insufficient, Aug. Beer's Introduction to the Higher Optics‡ will prove of service. In the choice of an instrument it is in the next place to be noted that the upper Nicol's prism should be placed over the ocular, and not between the objective (in the more restricted sense of the word) and the so-called collective. Amongst instruments constructed with the latter arrangement I have found nothing better adapted than this for minute and difficult investigation. Böttger, of Berlin, originally furnished the best Nicol's prisms for these purposes; more recently, however, Hartnack, in Paris, has constructed an admirably perfect instrument, arranged according to a method described by him and Prazmowski in the "Annales de Chémie et de Physique," 4e série, T. vii.

The microscopic image can be rendered still more beautiful by distributing the muscular fibres upon a plate of gypsum or mica, attached to the stage by means of Canada balsam, Dammar resin, or Jeffrey's solution of mastic and caoutchouc in chloroform. By appropriate inclination of the gypsum or mica plate a colored field is obtained, from which the muscles are projected, tinted with different colors, varying in proportion as their inclination on the plate increases or diminishes the difference of the paths which the rays respectively pursue. This experiment has the additional advantage, that the isotropal portions do not entirely vanish as in the dark field, but remain apparent, tinted with the color of the ground. The most beautiful effects are obtained when the thickness of the little plate is so proportioned that when the prisms are parallel to one another or crossed, it presents a beautiful purple color; the muscular fibres then appear blue or yellow, according to their inclination. Amongst the different purple

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* *Ueber die Muskelfasern der Mollusken, Sitzungsberichte der Wiener Akademie,* Band xxxix., s. 566.

† The fibres of the adductor muscle were originally erroneously regarded as smooth muscular fibres; that is to say, the substance of which is doubly refracting, but in which neither sarcous elements nor isotropal intervening substance can be distinguished.

‡ Brunswick, 1853, 800.

tints which can be obtained, that is the best which first appears in increasing divergence of the rays with crossed prisms, and which corresponds to the purple which is exhibited by Newton's color glass in reflected light at the limit between the first and the second system of rings. It furnishes in particular the most sensitive field; that is to say, small differences in the divergence of the rays occasioned by doubly refracting bodies lying upon the plate are rendered manifest by relatively great changes of color. From preliminary investigation with the polarizing microscope it is easy to discover, out of a series of gypsum or mica plates of various thicknesses, those that are best adapted for this purpose, attention being paid not only to the colors themselves, but to the amount of change of color occasioned by small accidental variations in the thickness of the sections. If the little plates which are used for preserving the preparation contain air between their lamellæ, which collects into bubbles in the preliminary immersion in oil of turpentine, this can be expelled by boiling in turpentine, and allowing it to remain in it till cold. It may then be transferred to the balsam or varnish, with which it and the muscular fibres lying upon it are to be enclosed.

CHAPTER VII.

THE HEART.

By F. SCHWEIGGER-SEIDEL.

THE muscular tissue of the heart presents certain peculiarities which connect it with the structure of those muscles that are subject to the will, whilst, on the other hand, in certain not unessential points it presents characters that are perfectly unique.

The structure is apparently fibrous, although the slightest examination shows that it is impossible to exhibit fibres corresponding to the elements

Fig. 58.

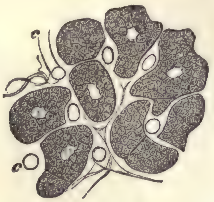

Fig. 58. Small portion of a transverse section through the muscular tissue of the heart. *c*, capillaries.

of the ordinary muscles. When it is broken up, we for the most part obtain only portions of thin fibrous-like structure, because the fine muscular fibres, dividing frequently and anastomosing with one another, form a close and continuous network.* The contractile substance is transversely striated, sometimes contains fat drops even when apparently healthy, and presents nuclei that are arranged at tolerably regular distances from one another. In the several round or oval disks which are found in sections perpendicular to the direction of the fibres, the nucleus is always in the centre,† excepting in those cases where, on account of the thinness of the section, disks without nuclei happen to be exhibited (fig. 58). The more or less wide fusiform spaces of the contractile substance in which the nuclei lie are filled in the larger specimens with a granular mass, which sometimes (in man) is of a yellow color (fig. 59).

The interpretation of the nature of the so-called muscular fibres of the heart is different from that applicable to those of the voluntary muscles. Weismann ‡ first established, from extended researches in comparative anatomy, that the relations in question are not the same for all the Verte-

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* The anastomosing muscular fibres of the heart, which had already been depicted by Leeuwenhoek, were rediscovered by Kölliker. See his *Mikroskopische Anatomie*, Band ii., pp. 209 and 483. Remak also described the peculiar characters of the muscular tissue of the heart in Müller's *Archiv* for 1850.

† Donder's *Physiologie des Menschen*, 1859, p. 23.

‡ *Archiv für Anatomie und Physiologie*, 1861, p. 42.

brata. In Lizards, Amphibia, and Fishes he found the several segments of the cardiac musculature to be formed of closely approximated elongated and fusiform cells, the substance of which presented transverse striæ (fig. 63). In Mammals, Birds, and Reptiles, on the other hand, although an analogous cellular structure could be demonstrated during the embryonic period, yet the anastomosing fibres of the heart must always, he thought, be regarded as formed from the coalescence of isolated cells. Kölliker and Aeby * opposed this view, and the latter observer even found the muscular fibres of adults to be divided into separate portions by transverse septa. But Eberth † has recently made an important step in advance, by showing that in two of the above-named groups of Vertebrata a separation of the several cells from one another occurs in the fully developed condition of the muscular tissue of the heart; so that what was commonly regarded as a single fibre turns out to be a complex structure composed of one or many nucleated transversely striated muscle cells. ‡ Here, therefore, in opposition to the term fibres, applied to the structural elements of the ordinary

Fig. 59. Fig. 60.

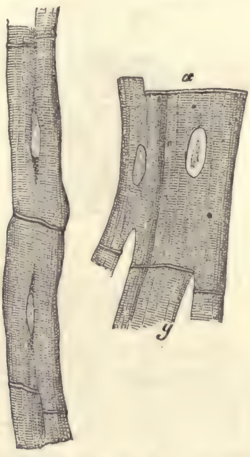

Fig. 59. Muscular fibres from the heart of Man, divided by transverse septa into separate nucleated portions. From a preparation preserved in alcohol after having been macerated in a 1 per cent. solution of potash, and in glycerine.

Fig. 60. Two laterally adherent muscle cells from the Guinea-pig. From a specimen that had been treated with acetic acid and solution of common salt.

muscles of the trunk, we may speak of chains of muscle cells or muscle-cell trabeculæ. The difference above referred to between the several groups of animals amounts only to a dissimilar mode of arrangement of the muscle cells, the independency of which in the heart still remains certain. As a proof of this statement, it happens that especially in Mammals we are able

* *Zeitschrift für rationelle Medicin*, 3 R., Band xvii., p. 195.

† Virchow's *Archiv*, Band xxxvii., p. 100.

‡ As long as a division of the cells from one another can be generally demonstrated we can obtain no correct estimate of the degree of coalescence that has taken place; hence it is not easy to discover the difference that exists between the statements made by Kölliker in the fifth edition of his *Handbuch der Gewebelehre*, and those advanced by Eberth. Kölliker now admits that the coalescence of the cells is somewhat less intimate than he had stated it to be.

to render the limits of the several cells apparent, and to obtain these in an isolated state. The best means for this purpose is the nitrate of silver, with subsequent application of caustic potass, by the employment of which Eberth was able to split up the muscular substance of the heart into separate prismatic portions, corresponding with the black lines that come into view after treatment with silver, and result from the staining of the connecting substance between the cellular elements. But we may also convince ourselves that, by the application of other means which render the tissue transparent, the muscular fibres are separated into distinct portions by highly refractive transverse lines, and that each of these divisions contains a nucleus. The want of transparency of the contractile substance usually prevents the delicate boundary lines of the cells from being discerned. But in all experiments in which isolation of the fibres is effected it is possible to obtain small nucleated portions of muscle, presenting similar appearances to those seen in fig. 60, the single septal line *a* being easily distinguishable from a fissure (*y*) produced by the previous manipulation.

The limiting surfaces of the several muscle cells are not plane. The transverse lines crossing the bundle frequently appear like a flight of steps. Eberth found the borders of the cells more or less regularly dentated. I have, however, observed them to be smooth, and believe the difference to

Fig. 61.

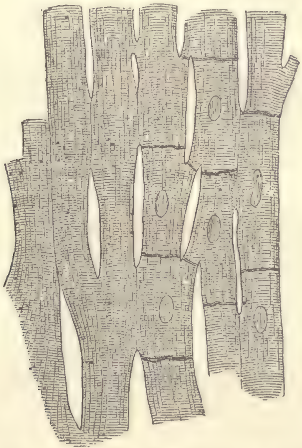

Fig. 61. Anastomosing muscular fibre of the heart, seen in a longitudinal section. On the right, the limits of the separate cells with their nuclei are exhibited somewhat diagrammatically.

be occasioned by the circumstance that the muscle substance sometimes comes under observation in the contracted, coagulated condition, as after treatment with nitrate of silver, and sometimes in the swollen, distended condition, as after treatment with acetic acid. Other irregularities of form appear to be due to the pressure which the muscle cells exercise upon one another. Every muscle cell contains a nucleus, occupying a central position, or two or more rarely several nuclei may be found, which sometimes lie in close relation to one another, and are of smaller size, thus appearing to proceed from the division of a single one. If the nuclei be widely separated from one another, the question arises, which it is not necessary here to consider, whether the several nucleated cells represent stages of development,

or whether there is a disappearance of the cell wall, or, in other words, that it has become incapable of recognition. In adults the solitary nuclei have a length of about 0·014, and a breadth of about 0·007 millimetres; whilst the muscle cells themselves measure, on the average, 0·050 to 0·070 millimetres in length, and 0·015 to 0·023 millimetres in breadth. The cellular elements are, for the most part, united to one another in the longitudinal direction, but in various parts they send off short lateral processes, which coalesce with those of neighboring cells, and in this way form the anastomoses that occur between the longitudinal fibres. The cells are only placed in direct apposition to one another, in a transverse direction, in those parts where the stronger muscular trabeculæ are formed. If, however, we consider the abundance of capillaries which, together with nerves and connective tissue, traverse the muscle substance in Mammals, we shall arrive at the conviction that it is impossible for any material to be of a more compact nature. Sections in various directions establish this most satisfactorily, and transverse sections, made from well-hardened hearts (Fig. 58), are admirably adapted for the purpose. But in fine longitudinal sections, numerous larger or smaller fissures, arranged in a stellate manner, may also be seen, and so fine that they have been described by some observers as fissures or spaces within the muscular fibres.* Varying conditions of contraction of the musculature naturally produce variations in the appearances presented. The fissures between the muscle cells are filled not only by the capillaries, but by a very delicate connective tissue, which, in the form of a perimysium, constitutes sheath-like investments, and appears to consist of isolated branched cells. I have not been able to discover a proper sarcolemma, *i. e.*, a special delicate investing membrane capable of isolation, around the muscle cells, and therefore, in common with other observers, wholly deny the existence of such a membrane investing the muscular fibres of the heart, or, at least, maintain that, if present, it can be demonstrated only with the greatest difficulty.† Nevertheless, the cells of muscle, like all other naked cells, must possess a peripherical investment. Independently of the above-mentioned elementary division into fibre cells, the muscular tissue of the heart splits up into coarse subdivisions. By means of septa proceeding from the perimysium, thick fasciculi or bundles are sometimes formed, which, as the well-known columnæ carneæ, are particularly well marked in the auricles. In the walls of the ventricles, on the other hand, the arrangement is rather of a lamellar character, several thin expansions of muscle being so applied to each other as to form a thicker plate, which is visible even to the naked eye.‡ The thinner lamellæ are either connected with one another by extremely delicate connective tissue, or there exists between them certain smooth-edged fissures, which may be followed for some distance, both in

* Remak, *loc. cit.*, *Rindfleisch Lehrbuch der Pathologischen Gewebelehre*, 1866, p. 73. Eberth, in accordance with this view, represents longitudinal fissures as existing in the muscle cells; but it may be seen in his Fig. 13, that these really indicate the line of union of two adjacent cells. Moreover, Eberth does not appear to attribute sufficient importance to my view of the natural fissuring of the muscle; at least, at p. 121, he observes that the muscular network of the mammalian heart does not exist to the extent attributed to it; but that the appearances seen may frequently be produced by manipulation.

† As to Winkler, who maintains the presence of a sarcolemma in the *Archiv für Anatomie und Physiologie* for 1867, it is obvious from his account of the appearances presented on transverse section, that he really treats of the sheaths of the perimysium.

‡ See Henle, *Handbuch der Systematische Anatomie*, Band iii., Abth. 1; *Gefässelehre*, p. 54, Figs. 40 and 44.

regard to length and depth. These fissures, to which Henle has drawn attention, are in my opinion deserving of particular notice. I find that they are lined by a very delicate membrane, composed of flat cells, the contour lines of which, after treatment with nitrate of silver, appear in the form of a black pattern. Moreover, it is possible to raise up and isolate this membrane after short maceration, which has confirmed me in the opinion that many observers have considered it to represent the sarcolemma. The fissures, in fact, occur in the connective tissue, as may be seen at their angles, and have in rabbits, where, I think, they can best be seen, a length of from 0·06 to 0·25 millimetres. We shall return, however, to this subject hereafter.

The arrangement of the muscular bands in the wall of the heart—the so-called lamination of the cardiac musculature—cannot be fully treated of in this work, since it possesses no histological interest. The careful investigations of C. Ludwig, Pettigrew, Winkler, and others, have, however, shown how complex these arrangements are; and, according to Henle, in addition to all these there must still be added the varieties due to individual differences. The results of accurate examination seem to show that the musculature of the auricles, speaking generally, is divisible into two layers, arranged at right angles to each other, of which the external is circular, but in the case of the ventricles the arrangement of the fibres cannot be described in so simple a manner. We must probably seek for the immediate cause of the spiral arrangement of the muscular bands that here exist in the history of its development, as it is well known that at an early period the cardiac tube forms not only a loop, but a spiral curve, through which necessarily a deviation in the course of both the longitudinal and transverse fibres will be occasioned. Sections made through the wall of the ventricle, in a direction perpendicular to the surface and parallel to the longitudinal axis, exhibit, both externally and internally, longitudinally running bands, whilst the median portion presents transverse sections of the fibres; consequently we can here, though only quite generally, distinguish the two chief directions they pursue.

The connective tissue is closely connected with the muscular substance of the heart, and presents at some spots a remarkable condensation; it is arranged in well-marked layers—this is particularly the case in the so-called fibrous rings at the cardiac orifices, and in a lesser degree at the apices of the papillary muscles, both being points which constitute the origin, or perhaps the termination, of muscular fasciculi. The fibrous rings are composed of very strong fibrous tissue, traversed by exceedingly fine elastic fibres, and sometimes assume to some extent the character of cartilage, the appearances presented resembling those found in true cartilage, at its point of transition into perichondrium. To these differences, which are by no means essential, the somewhat discordant statements and descriptions made by various authors may be ascribed. At the cardiac orifices the fibrous tissue enters into the formation of the valves, and in the papillary muscles it passes immediately into the tissue of the chordæ tendineæ, though always sharply separated from the tissue of the endocardium.

The endocardium forms a membranous lining to the cavities of the heart, but is not everywhere of equal thickness. It participates in the construction of the valves, and is composed of several layers. Its proper basis is formed of an elastic layer, which contains networks of elastic fibres developed to a variable extent, with a corresponding variation in the quantity of connective tissue. The external layer is the loosest in texture. Its internal surface is lined by a layer of nucleated polygonal cells, resting upon

a peculiar close-textured lamella of elastic fibres, which constitutes the endothelium of the cardiac cavities.

It may be added that the simple elastic lamina usually adheres closely to the muscular wall itself by means of a layer of connective tissue, whilst the muscular tissue aids in the formation of the endocardium by giving off to it both smooth and transversely striated fibres.

The smooth muscle cells are introduced between the elastic lamellæ, but do not form a continuous layer, being arranged in separate bands, which vary in size, and sometimes attain a thickness of 0·10 millimetres. The several layers of the muscle cells in these fasciculi do not all pursue the same direction, though they generally appear to be divided transversely when the section has been made perpendicularly to the axis of the heart. These statements are true at least in regard to the endocardium of the septum ventriculorum of man, in which smooth muscular tissue is very distinctly visible.* Moreover, the more externally situated transversely striated muscular tissue of the endocardium does not form a continuous or uniform layer, on which account it may easily be overlooked, or may be regarded as belonging to the muscular layers in general. That the latter is not the case, however, is obvious from the circumstance that the muscular elements in part possess special peculiarities, and also that the endocardial layer is separated from the general musculature of the heart by connective tissue, lymph vessels, and networks of nerves.

Moreover, we find in the endocardium *per se* all the usual layers entering into the composition of the vascular walls, and may therefore very correctly, with Luschka,† identify the endocardium with the whole vessel, and not simply with its tunica intima. It remains to be remarked that the above statements are not applicable to the auricles, since their endocardium, although it possesses considerable thickness, and is remarkably rich in elastic tissue, does not present any proper muscular layers, though here and there a few smooth muscle cells are discoverable. The transversely striated muscle of the endocardium of the ventricle occurs in two forms, either as the well-known Purkinje's fibres, or as a wide-meshed network of muscular bundles, the elements of which are distinguished from those of the heart by their proportionate size, being broader and shorter. As regards the gray gelatinous-like fibres recognizable by the naked eye, which Purkinje described in 1845 as being situated under the endocardium of the calf, they must partly be considered as a peculiar motor apparatus, and partly as an embryonic form of the muscular tissue of the heart.‡ The fibres are united to one another in the form of networks, and are composed of more or less prismatic segments (granules), having a diameter of from 0·05 to 0·10 millimetres, each of which consists of a cortical layer of transversely striated fibrillar muscle substance, and a hyaline axile material containing one or two clear nuclei. Some observers regard the transversely striated mass as an intermediate substance, within which are deposited transparent isolated cells; whilst others, with whom I agree, regard each granule as a muscle

* Kölliker denies positively the presence of smooth muscular tissue in the endocardium (*Mikroskopische Anatomie*, Band ii., p. 493). Nevertheless, in regard to the localities referred to, no doubt can exist of the correctness of my statement.

† Virchow's *Archiv*, Band iv., p. 171; and *Anatomie*, Band i., Abth. 2, p. 380.

‡ Besides the work of Purkinje (Müller's *Archiv*, 1845, p. 294), reference may be made to the statements of Kölliker, Hessling, Reichert, Remak, Aeby, Obermaier, and Lehnert. More exact and extended references to the literature of the subject will be found in the last-named authors. Obermaier, *Archiv für Anatomie u. Physiologie*, 1837, pp. 245 u. 358; Lehnert, Max Schultze's *Archiv für Mikroskopische Anatomie*, 1868, p. 26.

cell, in which (as in a certain stage of development) only the peripheric layers have undergone conversion into contractile substance.

In what relations these segments of the fibres of Purkinje stand to the cardiac muscle in its fully developed condition, is a subject that can only be elucidated by a knowledge of the history of development; but it may here be remarked that various observations have been made, which agree in showing that the fibres of Purkinje pass directly into ordinary muscular bands, and that in some animals their place can be supplied by ordinary muscular tissue. The controversy whether this or that animal possesses the fibres of Purkinje is therefore of small importance, because the differences depend merely upon the various forms presented by the endocardial muscle.

A division of the stronger fibres, as we have already seen, does not occur here, whilst they are for the most part surrounded by a well-marked sheath of connective tissue. These sheaths, when penetrated by an injection pipe, sometimes become filled with injection, and then form a wide-meshed network which it is impossible to mistake for the vessels of the lymphatic system (Eberth).

As already indicated in discussing the internal membrane of the heart, we have to consider the *valves*. These indeed are usually considered to be duplicatures of the endocardium, but this expression is not absolutely correct. The substance of these valves consists essentially of two lamellæ, a fibrous and an elastic; the former is directly continuous with the fibrous rings, the latter in the case of the venous valves is a prolongation of the endocardium of the auricle, but in the arterial valves it is a prolongation of the membrane lining the ventricular chambers. The free surface of the fibrous layer is invested by a thin membrane composed of cells which do not rest upon any special elastic substratum, except that perhaps the elastic element of the fibrous layer itself undergoes a slight thickening at the margin. In the semi-lunar valves the elastic layer is considerably thickened, whilst at the attached border of the venous valves the two layers disappear towards their apices, their place being supplied by the tolerably abundantly nucleated tendinous tissue of the chordæ tendineæ. The latter near the musculi papillares possess an external elastic layer with a delicate investing membrane composed of cells, which constitutes a prolongation of the endocardium.* At the apices of the valves muscular bundles pass directly into the endocardium of the auricle, and extend to a greater or less distance downwards, but in all instances are limited to the upper portion.†

According to the statements of Oehl,‡ small isolated muscles are present in the large tendinous cords of the left auriculo-ventricular valves. The fibres of Purkinje are continuous with the chordæ tendineæ. Villous processes or outgrowths are sometimes found attached to the valves (Luschka, Lambl.). In regard to the endocardium in general, it should be mentioned that the microscopic appearances which are found in various animals differ chiefly in the greater or less development of the elastic network of fibres. The foregoing description is chiefly taken from observations made on the heart of man.

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* Analogous observations were formerly made by Donders, in regard to the structure of the valves. I cannot agree with the statement of Luschka, that the valves are the direct continuation of the arterial wall, *Archiv für Physiologische Heilkunde*, 1856, p. 537; compare also Henle.

† Amongst the most recent investigations on the musculature of the auriculo-ventricular valves are to be enumerated those of Gussenbauer, *Sitzungsberichte der Wiener Akademie der Wissenschaften*, Band lvii., Abth. 1.

‡ *Mém. d. Acad. d. Scienze d. Torino*, Vol. xx., 1861.

The *pericardium*, in opposition to the endocardium, is a serous membrane, and possesses the general characteristic peculiarities of such membranes. The sub-serous tissue is occasionally marked by the presence of a large number of fat cells.

The *bloodvessels* are branches of the coronary arteries, and are distributed in the muscular substance, as well as to the pericardium and endocardium. The vessels of the last-named membrane extend, according to Luschka, into the valves. The capillary vessels distributed through the muscular substance of the heart are very numerous, the muscle cells themselves being enclosed in a network of vessels. The rootlets of the veins are formed by several capillary vessels uniting directly to form a thicker trunk; an arrangement by which, we may conclude, the discharge of the blood is facilitated.

In reference to the *lymphatics* of the heart, we possess recent investigations by Eberth and Belajeff;* and, as they have pointed out, a network of lymph capillaries of the ordinary kind may be distinguished both in the pericardium as well as in the endocardium, the meshes of which are sometimes large and sometimes small, and are usually arranged in a single layer, but occasionally, where the thickness of the membrane is considerable, in several layers. The endocardial lymphatic network of the auricle is continued by means of a few finer tubes upon the auriculo-ventricular valves, and reaches nearly to their middle. In the same way a few lymph tubes may be traced as prolongations of the network of the endocardium of the ventricle into the semi-lunar valves. In the muscular substance of the heart itself the above-named observers found, in opposition to Luschka, that the lymph vessels were "not so numerous," whilst I conclude, from my own researches, that the muscular substance of the heart stands in still closer relation to the lymphatics than appears from their statement, because I am of opinion that the formerly described fissures of Henle found in the muscular substance must be regarded as a portion and continuation of the lymphatic system. But since these fissures are connected at many points with one another, they form a canal system, permeating the muscular substance to an extent which certainly cannot be termed sparing. It has already been mentioned that the smooth fissures are covered with a delicate membrane analogous to the endothelium of the lymphatics, to which it must also be added, that it is easy to follow sub-pericardial lymph vessels and their prolongations into the lacunar system. That this system cannot be injected through the vessels constitutes no objection to our view. On sticking an injection pipe into the muscular substance of the heart, the fluid penetrates between the several elements of the muscles into the perimysium, and may become widely diffused, so that with slight pressure we may even see the injection penetrating into the lymph vessels of the pericardium without any evident rupture or extravasation. A complete injection of the lacunæ cannot be obtained in this manner. It is observable that the lymphatics of the muscular substance are not always in the form of fissures, but sometimes assume a tubular form, dependent upon the amount of injection forced in, and upon the degree of contraction of the muscular substance.

In regard to the finer distribution of the *cardiac nerves*, which is of peculiar physiological importance, little is at present known, and our knowledge is particularly defective in reference to the more intimate histological

* Virchow's *Archiv*, Band xxxvii., p. 124.

relations of the fibres springing from various sources and distributed to the different tissues.

The nerve fibres proceeding from the plexus cardiacus lie in mammals beneath the pericardium, but in part also they are found in the septum ventriculorum, where they run in the substance of the muscular mass and in the spaces between the two ventricles. Their distribution under the pericardium is independent of the vessels, and it even appears in some animals that the nerves cross the superficial muscular fasciculi and the vessels at right angles, as is clearly shown in the illustrations given by Lee.*

The isolated, somewhat flattened fibres, which intercommunicate by means of delicate fasciculi, consist chiefly of non-medullated nerve fibres. The double-contoured fibres vary in relative proportion, but are usually only sparingly present. The nerves enter into communication with ganglion cells. These, united into groups, lie on the external surface of the fasciculi of fibres, and sometimes form small detached ganglia, which are connected with the nerve by a peduncle. Accumulations of cells of materially larger size do not occur, whilst in particular the enlargements of the nerves perceptible to the eye are occasioned simply by the penetration into their substance of connective tissue, accompanied by large vessels.

The relation of the fibres to the ganglion cells can be better studied in the cardiac nerves of the frog than in the sub-pericardial nerves of mammals, as the former spread out in the thin interauricular septum, and are very well known in regard to their course of distribution, in consequence of several special works having been devoted to them (C. Ludwig, Bidder). The greater number of ganglion cells exhibit the structure peculiar to the cells of the sympathetic, in which from one and the same pole, besides the so-called straight fibre, there originates also the spiral fibre of Arnold and Beale, which has elsewhere been fully described. Besides these, however, as has been shown by various observers, true bipolar cells are present, and, lastly, also ganglion cells, characterized by the peculiar mode of their arrangement, which, if we accept the view of Auerbach,† are found "in opposition,"—that is to say, two pear-shaped cells lie in a common sheath with their flat sides applied to one another, whilst the nerve fibres issuing from their pointed extremities course in opposite directions. The approximation of such binary cells being very close, especially when they are examined in the fresh condition, they may easily be mistaken for simple bipolar cells. No spiral fibre is here present.

Auerbach found this form of ganglion cell in the plexus myentericus, Bidder in the auricular septum, and I myself in other sympathetic ganglia. According to my views, those cells from which two straight fibres can be seen to issue, belong to the same category, since as many even as three small ganglion bodies may be found invested by a common capsule.

Since the influence of the nerves on the activity of the heart has been more accurately investigated, the view has generally been admitted that the difference between the vagus and the sympathetic, or, in other words, the difference between the inhibitory and the exciting fibres, is to be sought for in the circumstance that the one acts directly on the muscular substance, the other only indirectly through the intervention of the ganglion cells. The latter is supposed to be the mode in which the vagus acts, though no positive proof of the fact has hitherto been adduced.

Kölliker, indeed, has convinced himself from anatomical investigation that the vagus stands in no direct relation with the ganglion cells, but other observers do not agree with him; and very recently Bidder,‡ who has also examined the subject anatomically, has stated that the spiral fibres are fibres of the vagus passing to the

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* R. Lee, *Philosophical Transactions*, London, 1849, Plates ii. and iii.
† Virchow's *Archiv*, Band xxx., p. 458.
‡ *Archiv für Anatomie u. Physiologie*, 1868, p. 1.

ganglion cells, whilst the straight fibres are given off by the cells, and are destined to be periphérically distributed. If, however, Bidder rests his view exclusively on the results of sections of the nerves made in frogs, his evidence is diminished in value to some extent, because in these animals the Rami Cardiaci are the only nerves which pass to the heart; and consequently, when they are divided, not only the inhibitory, but the exciting fibres would undergo degeneration.

The further distribution of the nerves in the muscular substance of the heart is difficult to follow, as they undergo rapid subdivision, or, at least, but few trunks can be seen. Hence it follows that the fibres are delicate and non-medullated. It is generally acknowledged that ganglia are distributed in the muscular substance. If, however, this be admitted on the authority of Remak,* it is to be remarked that he observed their presence under the microscope only in the case of the calf. I have not been myself successful in discovering such ganglia lying between the fibres in the proper muscular substance, and can only admit that they may be found on a few traversing trunks or branches.

Friedländer† maintains that large numbers of ganglion cells are present in the muscular substance of the heart of the frog, as he believes he has demonstrated the constant existence of such cells in still pulsating portions of muscle, in which there were not, in some instances, more than two or three muscular fibres. His statements, however, are not sufficiently precise. He has given no description of either the size, form, or appearance of the supposed ganglion cells, and has made no investigations to show their connection with nerve fibres.

We possess a few observations respecting the mode of termination of the nerves in the muscular tissue of the heart, that have been made by Kölliker and Krause. Kölliker considers that in the frog the pale nucleated fibres running on and in the secondary muscular bundles terminate in the same mode as the nerves of the voluntary muscles; whilst Krause states that "the double-contoured nerve fibres of the cardiac muscle end in motor terminal plates; and hence the peculiar operation of the cardiac nerves receives no explanation from the mode in which they terminate."‡

That the relations of the cardiac nerves must differ from those distributed to the muscles of the trunk is probable on *à priori* grounds, from the different arrangement of the muscular elements; for, as the several muscle cells preserve their independence, it is easy to conceive that their mode of innervation would be peculiar, and would present an analogy to that of the smooth muscular tissue. Further inquiry is requisite to determine the precise mode in which the ultimate distribution of the nerves is effected, but the following remarks may be provisionally made for the purposes of comparison with the arrangements presented by other muscles.

The nerves run in the connective tissue accompanying the capillaries and occupying the fissures between the muscle cells, and appear in the form of delicate nucleated fibres, resembling those which are elsewhere seen to constitute the peripheric terminations. It is difficult, even in very thin layers of muscle, to discover the extremely delicate fibres. The nuclei of the capillaries, of the nerves, and of the muscle, however different their characters may be, confuse the microscopic image to so great an extent that no other course is left but to isolate the nerves by dissolving out the network of muscle cells.

If specimens be taken from the middle of the ventricular wall of Mammals, we may obtain, in successful cases, numerous nerve fibres, though

* Müller's *Archiv*, 1844, p. 463.
† *Untersuchungen aus der Physiologische Laboratorium in Würzburg*, Heft. ii., 1867.
‡ *Anatomie des Kaninchens.* Leipzig, 1868, p. 178.

usually only in fragments, and may see how frequently they divide, and, with great clearness, the mode in which they form networks (Fig. 62). The divisions are, in some parts, very numerous (a), though the lateral branches are for the most part torn off. We seldom meet with such a case as is represented at b, and when seen, there must always remain a doubt whether a natural termination is under observation, because the fibrils issuing from the second nuclear swelling are so fine that no sure ground is afforded to determine whether or no they are broken off. In the Frog, the arrangement is so far different that no capillaries exist in the muscular mass, and the individual bundles are composed of closely compressed fusiform cells. In

Fig. 62.

Fig 62. Isolated nerve fibres from the muscular substance of the wall of the ventricle. From the Dog. Magnified 500 diameters.

Fig. 63, two trabeculæ are exhibited from the auricle, partially detached from each other. Fine nerve fibres, with the ordinary nuclei, intervene between them, and, after frequently undergoing subdivision, become closely applied to the muscular fasciculi. (The branch a runs beneath the fasciculus.) Fine fibres are, as usual, given off from the characteristic triangular nuclei, which penetrate into the interior of the fasciculus, and it may then easily be seen that the nucleated fibre c lies in a space between the muscle cells. By carefully isolating the tissues, very fine branched fibrils may be exhibited, which might be regarded as nervous in their nature, even without any direct connection with undoubted nerve fibres being discoverable. Such fine fibrils sometimes adhere firmly to the muscle cells.

Notwithstanding the doubts that exist on some of these points, it may be regarded as well ascertained that the finer branches of the cardiac nerves lie between the proper elements of the muscle, and so come into immediate contact with the contractile substance which is here destitute of sarcolemma.

As to what proportion the number of terminal nerve branches bear to the number of muscle elements, no positive statement can at present be made. I have not been able to observe any such direct connection between the nerves and the nuclei of the muscle cells as has been stated by Frankenhäuser in regard to the smooth muscles.*

Fig. 63.

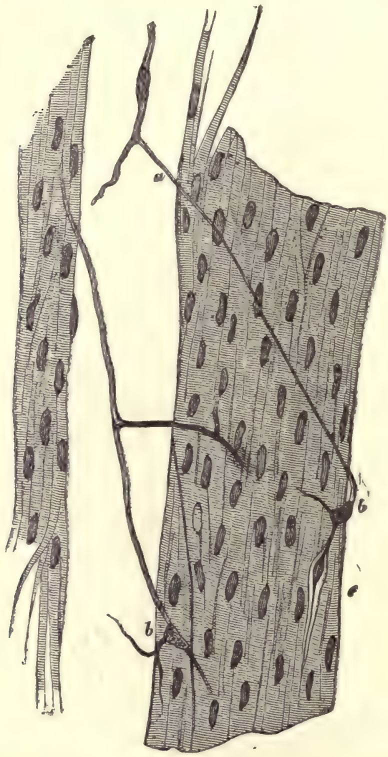

Fig. 63. Trabeculæ of muscle from the auricle of the Frog, with the nerves.

It still remains to notice other parts in which ramifications of the cardiac nerves occur, and of these the first that may be mentioned is the pericardium, in which, as in other serous membranes, networks of fine fibres are present. And, secondly, the endocardium, in which a very considerable development of nervous tissue exists. This distribution is not exclusively connected with the presence of muscular layers, since, besides motor, we must certainly admit the existence of other nerves with different endowments. The latter terminate in the inner laminæ of the membrane; but their finer branches, in consequence of the elastic tissue present, are only to

* To enter more minutely on this subject, and to give the details required for making special investigations in it, would lead us too far, and the consideration of these points must therefore be reserved for discussion elsewhere.

be discovered with difficulty, and require the application of chloride of gold.* They are nucleated, and form networks in the membrane which are analogous to those ordinarily found in serous membranes, except that the meshes are much narrower. Since, however, there is no regularity in their distribution, any attempt at comparative measurement would only be applicable to special instances. The nerves terminate in a manner essentially similar to those of serous membranes generally, though it is here extremely difficult to arrive at any positive conclusions.

The plexus of coarser fasciculi lying in the sub-serous connective tissue, and therefore beneath the muscular layer of the endocardium, and which can easily be brought into view, must be distinguished from the fine networks of fibres above described. Isolated fibres are given off from them, which partly end in the muscles and partly enter into the formation of the above-mentioned fine networks.

* The above statements are based on hitherto unpublished investigations that have recently been made under my direction by Dr Schmulewitsch.

CHAPTER VIII.

THE BLOODVESSELS.

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In adult vertebrate animals the essential constituent of the bloodvessels is a tubular system formed of a single layer of flat cells, or of a delicate nucleated membrane, termed the endothelial tube by His,* the perithelial tube by Auerbach,† and the cell membrane by Remak.‡ This tube is the least variable part of the vascular walls, and is present alike in the finest bloodvessels, in the largest trunks, and in the dilated portions of the vascular system—the heart and the several sinuses—however much the other constituents of the vascular wall may vary. In a few organs, however, as in the spleen of Mammals, in the pulmonary organs of the Cephalophora, and in the gills of Crustacea, the passages through which the blood courses appear to be destitute of a proper wall.§ The capillaries and smaller veins are formed of this tube alone, the elementary constituents of which are delicate, flattened, more or less fusiform, or polygonal cells, composed of a nucleus with surrounding protoplasm, and arranged for the most part parallel to the long axis of the vessels.

In the heart and arteries, and in most of the veins, this cell tube is invested by connective tissue and by elastic and muscular elements, which are frequently arranged in layers, but are often also irregularly combined into a tunic, that in opposition to the internal cellular membrane may be called the *external vascular coat* or *investing membrane.* The thickness of this membrane does not increase proportionally to the diameter of the vessel, as there are wide vessels with very thin, and small vessels with comparatively thick coats. Amongst the Invertebrata, as in snails and mussels, even the large lacunar blood spaces which surround the viscera are bounded only by a very delicate cellular membrane, which invests the various organs as an external epithelial tissue, similar to the epithelium of the peritoneum.

The smaller vessels have thicker walls in comparison with the larger, but the several components of the wall do not participate to an equal extent in producing this increase of thickness. It is chiefly effected by an augmentation of the muscular tissue, which becomes abundant in proportion to the diminution in the quantity of the elastic and connective tissue.

The tissues which form the investing tunics are arranged in layers, the thickness of which, as well as the order of their succession, undergo many variations.

The investing layer is limited internally by an elastic membrane termed

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* *Die Häute und Höhlen des Körpers.* Basel, 1866.

† Virchow's *Archiv*, Band xxxiii., 1865.

‡ Müller's *Archiv*, 1850.

§ Bidder, in his *Beiträge zur Gynäkologie und Geburtskunde, v. Holst*, 1867, has incorrectly denied the presence of an endothelium in the marginal veins of the placenta. See Eberth, Virchow's *Archiv*, Band xliii., p. 136, 1868.

the *internal elastic coat.* The external surface of this membrane is covered by a muscular layer composed of smooth muscular fibres, which are partly arranged in a circular and partly in a longitudinal direction. This layer is termed the *middle coat* in consequence of the position it occupies between the elastic coat on the one hand, and the *external coat* or *tunica adventitia*, composed chiefly of connective tissue and elastic fibres, on the other.

To these tunics must still be added a fourth connective tissue layer—*the internal tunic* or *internal longitudinal fibre layer*, which lies between the endothelium and the elastic internal coat, and which I shall term the *intermediate layer.* In the arteries it is only present in the larger vessels, and is gradually lost towards the periphery. In the veins it attains its maximum in some of the peripheral vessels, and diminishes towards the heart, so that it is almost entirely absent in such large vessels as the vena cava.

Besides the above-named elements the vascular walls contain elastic fibres and sheets, which sometimes appear as finer or coarser fibres arranged in a retiform manner, at others in the form of strong broad bands, and sometimes as fine striated lamellæ and membranes. The elastic fibres form a network extending through the whole thickness of the investing layer, the proportional development of which varies not only in different portions of the vascular system, but also in the different coats. Such fibrous networks attain a great development in the arteries on the external surface of the muscular tunic, where they often form a strong and tolerably well defined layer. (Henle's *external elastic coat.*)

VASA VASORUM AND NERVES.—The tunica adventitia of the large arteries and veins possesses arteries, capillaries, and veins which may extend even into the external layers of the muscular coat. The inner fibrous membrane is destitute of vessels.

Lymphatics have not hitherto been traced into the coats of the bloodvessels. The lymphatics of the endocardium only extend as far as the semilunar valves.*

In Amphibia and Reptiles, the large vessels, and especially the arteries, lie in the interior of immense lymphatic spaces, and are invested by the cell membrane of the lymphatics.

The perivascular spaces in the brain and spinal cord of Mammals, which were formerly regarded by His as lymphatics,† are, according to his more recent investigations, as well as mine, only lacunæ in the tissue, and possess no proper walls.

With the exception of the capillaries, the presence of nerves has been demonstrated in all vessels, even in the tunica adventitia of the non-muscular veins of the pia mater. These, partly consisting of dark-edged and partly of pale fibres, break up after they have traversed the tunica adventitia into a fine network. The fibres of this network, according to my observations on the small cutaneous vessels of the Frog, are of the most delicate description, whilst the network is of the closest character. I have not been able to convince myself of the precise mode in which they terminate, especially in regard to the muscles.

Ganglion cells occur in the course of some of the afferent nerve fibres, and in the coarser plexuses. Beale ‡ considers them to be very widely distributed. I have recognized them only in the inferior vena cava of the

* Eberth and Belajeff, Virchow's *Archiv*, Band xxxvi., 1866, p. 124.
† *Zeitschrift für wissenschaftliche Zoologie*, Band xv., 1865, p. 127.
‡ *Philosophical Transactions*, cliii., p. 562.

Frog, where they were first discovered by Lehmann.* Heaps of small, somewhat flattened, and closely compressed ganglion cells unite to form roundish nerve knots.

ARTERIES.

The arteries are distinguished from the veins by their thicker walls, resulting from the greater development of their muscular and elastic fibres. The thickness of the entire wall increases, though not proportionally to the increase of the calibre of the vessel. The thickness of the muscular tissue increases with the diminution of the calibre. The quantity of elastic fibres, on the other hand, increases with the calibre. The *cellular layer* of the arteries consists of fusiform or, occasionally, polygonal cells, which vary but little in diameter in the various vascular provinces.

ELASTIC INNER COAT.—The innermost layer of the external vascular coat—the elastic membrane of Donders, the elastic internal tunic of Kölliker, the elastic longitudinal fibre layer of Remak—consists in the finest vessels of a network of fine elastic fibrils, or of a delicate structureless

Fig. 64.

Fig. 64. Endothelium of the carotid artery of Man, after treatment with nitrate of silver. *a*, cells; *b*, clearer; *c*, darker intermediate spaces; *d*, intra-cellular circular and spotted markings.

elastic membrane, which, in collapsed or bent vessels, or when separated from its attachments, exhibits fine parallel, longitudinal, and transverse folds. It can be distinguished even in very fine tubes possessing only isolated muscle cells. Towards the larger vessels the membrane increases in

* *Zeitschrift für wissenschaftliche Zoologie*, Band xiv., p. 346.

thickness; small rounded or elongated spaces occur in it, and it now appears as a fenestrated membrane thickened with longitudinal rugæ (Arteria basilaris). In the larger vessels the fenestræ are more numerous; the membrane, in consequence, assumes the appearance of a network composed of fibres of varying thickness, or of a fenestrated membrane with plexiform thickenings. Large trunks, such as the axillary, carotid, pulmonary, crural, popliteal, and hepatic arteries, instead of a simple elastic membrane, possess two or three anastomosing lamellæ, or plexuses of elastic tissue, a clear, but slightly fibrous connective tissue filling up their interspaces.

INTERNAL FIBROUS COAT.—With the above membrane is associated a second, which, however, is not, as Henle * maintained, situated between it and the next coat, the so-called tunica media; but, according to the observations of Kölliker,† Gimbert,‡ and myself, occupies a position intermediate between the epithelium and the elastic inner tunic. Remak has designated this layer as the *innermost longitudinal fibrous coat;* Kölliker, as the *striated*

Fig. 65.

Fig. 65. Elastic internal tunic of the basilar arteries.

layer of the internal coat. This coat consists of a finely granular substance, with delicate fibrils running transversely and longitudinally. The greater part of this tunic is destroyed by the action of potash. Externally, this membrane becomes more distinctly fibrous, and gradually passes into elastic networks and membranes.

According to Langhans, § this layer is not distinctly fibrous in young persons, but indistinctly granular, the striation first becoming apparent after the membrane has attained a certain thickness.

The tissue of this membrane contains numerous fusiform and stellate cells, lying in anastomosing canals, with relatively large nuclei, and with either finely granular or quite homogeneous cell substance. Amongst these elements small granulation cells are sometimes found, respecting which it is a matter of doubt whether they are to be regarded as normal or pathological constituents. In some instances, the nuclei of the fusiform cells present so well marked a rod-like form as to lead to the supposition that smooth mus-

* *Allgemeine Anatomie*, p. 496.

† *Handbuch der Gewebelehre*, 5. Auflage, p. 583.

‡ *Mémoire sur la structure et sur la texture des Artères, Journal de l'Anatomie et de la Physiologie*, par Charles Robin, p. 536, 1865.

§ Virchow's *Archiv*, Band xxxvi., p. 197, 1866

cles are present. But, like Kölliker,* who first drew attention to them in the axillary and popliteal arteries, I have been unable to convince myself of the presence of smooth muscles in the internal coat of these vessels. On the other hand, I have met with isolated muscle cells in the internal longitudinal fibrous tunic in the hepatic and splenic arteries, and in the crural, at the points where they divide.

Muscular Coat.—The transition of a capillary into an arterial tube commences with the appearance of scattered transversely disposed fusiform muscle cells, immediately external to the endothelial tube, and between it and the tunica adventitia.

Fig. 66.

Fig. 66. Small artery from the brain of Man. *a*, tunica adventitia; *a'*, a nucleus of the tunica adventitia; *b*, muscle nucleus; *c*, elastic internal tunic; *d*, cell membrane formed of fusiform cells.

The muscle cells, which at first form only a single interrupted layer, gradually increase in number, and come to constitute an independent layer of cells, adjoining to and superimposed upon each other. Externally, this layer is, for the most part, sharply bounded by the external elastic tunic, or by the tunica adventitia, and internally by the inner elastic membrane.

I find that a short portion of the pulmonary artery and the aorta, im-

* *Zeitschrift für wissenschaftliche Zoologie*, Band i., p. 81, 1849.

mediately above the attachment of the semi-lunar valves, are destitute of muscle.

Many arteries possess no muscles whatever. Leydig * found none in the aorta of Balæna musculus, nor in the aorta and other larger arteries of Raja batis, Spinax niger, and Polypterus, nor in the basilar artery of the brain of Scymnus lichia, the fine cerebral arteries of which, however, contain distinct circularly arranged muscles.

With the exception of the largest arterial trunks, the muscular layers consist of finely granular connective tissue, containing scattered cells, and traversed by a few fine elastic fibrils, in which lie a number of muscle cells, more or less closely packed. In the more peripherically situated vessels the quantity of this intermediate substance diminishes, and the muscle cells are in closer proximity with one another. In the larger arterial trunks, as the aorta, pulmonary, subclavian, and carotid arteries, the intermediate substance is not only so abundant that the short and isolated muscle cells, and the smaller groups of such cells, are separated from one another by large intervening spaces, but the elastic tissue also attains its greatest development in the muscular layers. Associated with the fine and narrow-meshed elastic-fibre networks which traverse the fibrous, granular intermediate substance, are a series of lamellæ of tolerably even width, composed of elastic bands and fenestrated membrane. These, arranged at nearly regular

Fig. 67.

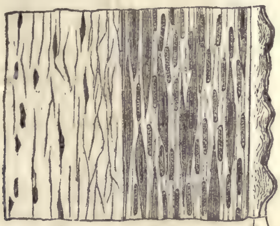

Fig. 67. Transverse section of the coats of the basilar artery. *a*, endothelium; *b*, elastic internal membrane; *c*, muscle cells; *d*, tunica adventitia.

intervals, constitute septa, dividing the muscular tunic into numerous layers. The lamellæ are connected by numerous oblique anastomoses, and are also continuous with the fine elastic fibres. They chiefly pursue a transverse direction.

In man, at least, there is always a layer of circularly arranged muscle cells, which, however, are strengthened by oblique or longitudinal muscular fasciculi, that are sometimes situated externally, sometimes internally, to the circular fibre layer, and sometimes occupy both positions.

Scattered longitudinally and obliquely disposed muscle cells are found in the descending thoracic aorta between the transverse muscular fibres. The large vessels that, on account of their loose connections, are easily moved, like those of the viscera of man and mammals, the arteria lienalis, renalis, umbilicalis, and dorsalis penis, are particularly characterized by longitudinal muscular bundles.

The longitudinal muscles of the arteries are chiefly situated in the tunica

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* *Lehrbuch*, 1857.

adventitia, especially in its internal and middle layers, where, however, they seldom form a continuous layer, but are united into fasciculi of greater or less strength (arteria renalis, lienalis, dorsalis penis). A well-developed longitudinal muscular layer invests the circular fibrous layer, which is also strongly marked in the arteries of the mesovarium of Batrachia. The adventitia of the crural artery contains a few short longitudinal fasciculi. According to Remak,* both in man and various mammals (ox, sheep, pig), small bundles of longitudinal muscles, apparent even to the naked eye as whitish masses, are recognizable on the external surface of the arch and thoracic portion of the aorta.† In oxen, sheep, and pigs, Remak was able to follow the longitudinal muscles as far as the iliac arteries, and in the sheep he found them in the pulmonary artery and its branches. In the arteries distributed to the viscera, Remak found external longitudinal mus-

Fig. 68.

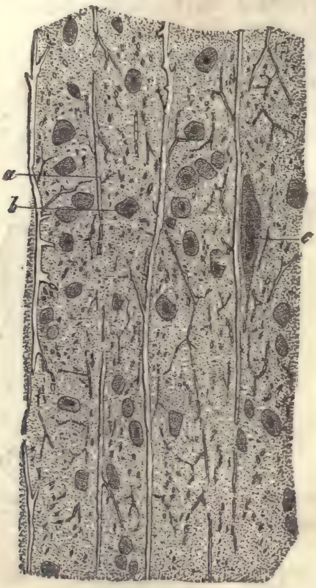

Fig. 68. Longitudinal section through the coat of the thoracic aorta. *a*, elastic plates; *b*, transverse muscles in section; *c*, longitudinal muscles.

cles only in the trunk and in the primary divisions of the superior mesenteric, the splenic, and renal arteries of oxen, but in the sheep they are scarcely perceptible in the arteria mesenterica. In both, the bundles are collected into a thick uninterrupted longitudinal layer.

I was only able to find internal longitudinal muscles in the form of isolated cells in the internal longitudinal fibrous tunic of the hepatic, splenic, and crural arteries. I was not able to discover them in the remaining abdominal vessels, nor in the axillary and popliteal arteries, where Kölliker believed he had recognized them.

* Müller's *Archiv*, p. 96, 1850.

† I can corroborate this statement in the case of the calf.

A delicate layer, composed of contractile longitudinal fibres, exists, according to Remak, in the internal longitudinal fibrous tunic of the renal, splenic, hepatic, and mesenteric arteries of man, the ox, sheep, and pig. These muscles, however, are only found near the origins of these vessels, and on the proximal side of the point at which the branches are given off from the trunk. In oxen, these muscles form thick, strongly projecting longitudinal cords that are crossed by strong circular fibres near the larger openings, and there constitute a kind of sphincter.

Through these longitudinal muscles the openings of the less fixed vessels, given off at acute angles, are probably kept contracted when, in consequence of the strong contraction of the discharging vessels, the passage of the blood is checked. This longitudinal fibre layer is absent in those vessels where, on account of their fixity, and the equality of the strength of the blood column, this provision is not required, as in the innominate, carotid, and subclavian arteries.

I have observed scattered longitudinal muscles in the tunica interna, at the points where branches are given off at acute angles, as at the division of the external iliac into the femoral and profunda arteries.

Distinct external and internal longitudinal muscles are only found in the extremely muscular umbilical arteries. The circular muscular layer is here lined internally by a continuous layer of longitudinal muscles, and externally by interrupted and slender muscular bundles, running in the same direction.

External Elastic Coat, and Tunica Adventitia.—The external elastic tunic of Henle * exists as an independent membrane in the smaller and medium-sized arteries, with few exceptions (internal spermatic, splenic, renal, hepatic, brachial, crural, popliteal and plantar arteries).

The basilar artery, the muscular tissue of which is poor in elastic fibres, loses this membrane completely, and presents instead a very loose network of fine elastic fibres in the tunica adventitia The dorsal artery of the penis contains similar and numerous elastic networks. The aorta, axillary, carotid, subclavian, and pulmonary arteries, whilst they present largely developed elastic laminæ in the muscular tunic, do not possess a proper external elastic membrane.

Speaking generally, this membrane is formed by a network of fine elastic fibres, which is sharply defined internally towards the muscular layer, but which externally anastomoses with the elastic network of the tunica adventitia. The remaining portion of the adventitia consists of decussating fasciculi of connective tissue, with networks of elastic fibres.

After what has been said, it is obvious that, whilst a description can be given which shall be applicable to individual arteries, and to groups of arteries, no general statement can be given that is appropriate to the entire arterial system; there is, in fact a certain antagonism between the elastic element of the tunica adventitia and that of the circular muscular layer, as is well shown in the case of the basilar artery. Still more frequently, again, there exists a certain antagonism between the muscles and the elastic elements of the circular muscle layer. If, in any vessel, the muscles preponderate, the elastic fibres diminish and recede towards the adventitia.

* *Allgemeine Anatomie*, p. 502; *Handbuch der Anatomie des Menschen*, Band iii., p. 73; *Gewebelehre*, von Kölliker; *Luigi Fasce*, *Istologia delle arterie e delle vene degli animali vertebrati.* Palermo, 1865.

The Veins.

Veins differ from arteries in possessing thinner walls, less elastic and muscular tissue, and for the most part a stronger tunica adventitia.

The Epithelial Layer consists of cells that, when compared with the corresponding structures in the arteries, present a more polygonal and less distinctly fusiform shape, and are consequently both shorter and broader. Their size varies in different regions.

Elastic Internal Membrane.—The veins, like the arteries, possess an elastic membrane, situated immediately beneath the epithelium, and apparent even in small vessels. This tunic never acquires the size and strength it exhibits in the arteries, and usually appears as a delicate and rather loose network of fibres, which, for the most part, run in a longitudinal direction, and but rarely, as in the larger trunks, undergo development into a fenestrated elastic tunic. In the iliac and crural veins this coat appears in some places to be split into two laminæ, which intercommunicate with one another by fine elastic fibrils. A delicate indistinctly fibrous connective tissue, containing longitudinally and transversely arranged short fusiform cells, occupies the interspaces of this network.

The internal longitudinal fibrous tunic is situated between the epithelial layer and the internal elastic membrane, as in the arteries, but is developed to a much less extent. In some veins it is almost wholly absent, as in those of the neck, the axillary vein, the vena cava, the mesenteric and portal veins, the vena azygos, and the branches of the pulmonary vein. The thickness of this layer by no means corresponds with the size of the vessel. Thus it is absent in the vena cava inferior, both above and below the liver, reappearing in the iliac vein, and increasing gradually in strength until the popliteal is reached, where it attains its greatest thickness. At this part the membrane often forms thickenings, which appear even to the naked eye as small elevations and transverse rugæ. On tracing it further towards the periphery its thickness will be found to undergo gradual diminution.

Its structure is essentially similar to that of the same layer in the arteries, with the exception that in many parts numerous muscles are present which fail to appear in the corresponding arteries. Thus the crural vein presents small bundles of longitudinal muscular fibres between the laminæ of its elastic inner coat, and the popliteal possesses in the same layer an internal longitudinal and an external transverse layer of muscular fibres.

Muscles.—In accordance with the presence or absence of muscles in the walls of the veins, these vessels are divided into the muscular and the non-muscular.

To the former belong the veins of the pia and dura mater, the veins of Breschet in the bones, the veins of the retina, the lower portions of the veins of the trunk opening into the vena cava superior, the external and internal jugular veins, the subclavian veins, and the veins of the maternal portion of the placenta.

In accordance with the arrangement of the muscular tissue, the veins may be divided into three groups; namely,—

Veins with longitudinal muscles, as those of the pregnant uterus.

Veins with an internal layer of circularly, and an external layer of longitudinally arranged muscular fibres of which examples are found in the vena

cava inferior, both in and below the liver, the vena azygos, and the portal, hepatic, internal spermatic, renal, and axillary veins.

The third group includes veins possessing an internal and an external longitudinal and a middle transverse layer of muscular fibres. Amongst these are the iliac, crural, and popliteal veins, the branches of the mesenteric veins, and the umbilical vein.

A fourth group includes the veins with circular muscular fibres, to which the veins of the upper and partly of the lower extremities, the smaller veins of the neck, the internal mammary vein, and the veins in the substance of the lungs belong.

The arrangement of the muscles is thus seen to vary even in the same vascular region. The middle-sized branches of the mesenteric veins contain, for instance, two longitudinal muscular layers with an intermediate circular layer, whilst, on the other hand, the vena porta possesses a feebly developed internal layer of circular fibres, and an external longitudinal layer of considerable thickness.

As regards the proportionate strength of the muscular coat, the veins of the lower extremity and vena umbilicalis occupy the first rank ; and then follow in succession those of the abdominal viscera, and of the upper extremity, which are about upon an equality ; and finally those of the thorax and neck.

The longitudinal muscular coat is most developed in the inferior vena cava below the liver, in the iliac, portal, renal, and mesenteric veins.

The thoracic portion of the inferior vena cava has no contractile fibres in man, the ox, sheep, pig, and rabbit, whilst the hepatic portion of the same vessel in these animals possesses a strong circular muscular layer.

In the superior vena cava of man, in opposition to that of the ox and sheep, there are no muscular fibres, and they first appear in the upper branches of the common jugular vein. Here, in consequence of the fixed position of the vessels, those obstacles are absent which render the passage of the current in the inferior cava difficult. On the other hand, according to Remak, in the superior cava of the ox and sheep there are internal transverse and external longitudinal muscles, an arrangement that may, perhaps, be rendered requisite by the different position in which the head is maintained.

The Tunica Adventitia of the veins, like that of the arteries, consists of bundles of decussating fibrils, the direction of which is for the most part longitudinal. As a general rule their diameter increases with that of the vessel, but there are many exceptions. The tunica adventitia of the veins is distinguished from that of the arteries by its greater thickness and the small amount of elastic fibres it contains, as well as by the presence of longitudinal muscles in certain vessels. The external layer of longitudinal muscles belongs exclusively to the tunica adventitia. To whatever extent the longitudinal fibres may be developed, they never form a distinct coat as in the tunica adventitia of arteries, but only a coarse network constructed of larger or smaller fibres, which are chiefly found in the middle and internal layers of the tunica adventitia, and diminish towards the outer. The limits between the layers of muscular and elastic fibres are never very well defined.

The Valves of the Veins cannot be regarded as true duplications of the internal tunics. The elastic finely fibrillated internal membrane covers only the convex surface of the valves. The proper substance of the valve is composed of finely fibrillated connective tissue with stellate and fusiform cells.

The muscular fibres which have been described by Wahlgren in the larger valves, I have not been able to discover with certainty.

The sacciform transparent appendages of the veins on the cardiac side of the valves of the veins (to be found in the axillary external and internal jugular and crural veins, as well as in the other branches), which, according to Remak,* consist exclusively of bundles of smooth muscular fibres, I find are not contractile.

CAPILLARIES.

Capillary vessels removed from living adult animals, and examined with due precaution, as, for example, those of the hyaloid membrane of Frogs, treated with the fluid of the aqueous, appear to be composed of a delicate, double-contoured, dull membrane, in which oval nuclei are imbedded at tolerably regular intervals. The parietes of these tubes are therefore not structureless. The capillaries of the hyaloid of the Frog appear to consist of a soft cloudy substance which in no respect differs from the substance of the delicate threads of protoplasm given off by the cells of the tunica adventitia.

Fig. 69.

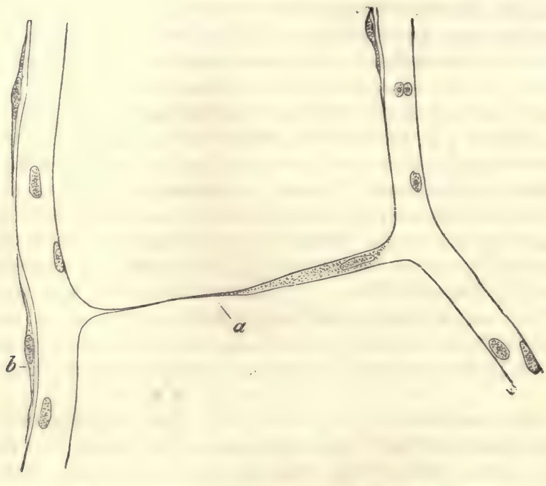

Fig. 69. Capillaries from the membrana hyaloidea of the adult Frog, showing a thread-like solid anastomosis between them. *a b*, cells belonging to the tunica adventitia.

In young living animals, as in tadpoles, we may still more easily convince ourselves that the capillary wall is not completely structureless, but that granules are distributed through it in a stellate manner, and that in its general appearance it closely resembles protoplasm. The wall here frequently appears uneven and provided with small teeth, or prolonged into fine partly solid and partly hollow funnel-like and, for the most part, non-nucleated pointed processes. The substance of these is always more granular than that of the rest of the membrane.

Such lateral processes are found also in adult animals, Stricker† having seen them in the nictitating membrane of the Frog, whilst I have also ob-

* *Ueber contractile Klappensäcke an den Venen des Menschen*, *Deutsche Klinik*, iii., p. 32, 1856.

† *Sitzungsberichte der Wiener Akademie*, Band xii.

served them in the hyaloid. Threads of a similar nature occasionally form connecting bridges between neighboring vessels. The diameter of these processes is often far less than that of the capillary from which they spring, and is insufficient for the passage even of a single blood corpuscle. These outgrowths, which act as vasa serosa, and as the youngest sprouts of growing capillaries, render it highly probable that even in adult animals a new formation of vessels occurs, though, perhaps, only to a limited extent.

Fig. 70.

Fig. 70. *a*, Small capillaries with fusiform cells, taken from the mesentery of Leuciscus; *b*, capillaries of the pecten of the eye of the Bird, exhibiting polygonal cells; *b′*, hyaloid membrane investing the capillaries; *c*, capillaries from the intestine of the Snail, showing irregularly lobed cells.

In many and especially in large recently formed capillaries, whether produced under normal or under pathological conditions, as, for example, in the membrane capsulo-pupillaris, the wall may be almost immediately broken up into finely granular fusiform protoplasmic masses.

A similar cellular structure may be rendered apparent in the capillaries

of adult animals by various modes of preparation. Thus Klebs* observed that in the urinary bladder of the Frog, after treatment with phosphate of soda, the nuclei of the capillaries were invested by a cloudy layer of protoplasm, which formed elongated fusiform bodies partly lying on the surface and partly imbedded in the substance of the membrane. Nearly coincidently in point of time, and apparently independently of each other, Hoyer,† Auerbach,‡ myself,§ and Aeby,‖ and more recently Chrzonszczewsky,¶ have by means of nitrate of silver shown that the wall of the capillaries is divisible into nucleated areas. The action of the nitrate of silver is to color the substance intervening between the cells of a brown or black tint, by which means the individual cells are brought into strong relief, and may be then isolated by treatment with a solution of potash containing 35 per cent. of the alkali (Aeby, Eberth).

A cellular structure was subsequently shown to exist in the wall of the capilllaries in almost all the organs of vertebrate as well as of many invertebrate animals, both by myself** and by Legros.††

The plexus demonstrated by Federn‡‡ in and upon the capillary walls, after treatment with nitrate of silver, is entirely different from the foregoing, from which it is distinguished by the irregularity of its meshes. Its nature has not been satisfactorily ascertained. The form of the cells lining the capillaries varies to a considerable extent. As a general rule it is different in vessels of different calibre. Small capillaries present cells that are more fusiform in shape; large capillaries, cells that are more polygonal. After treatment with nitrate of silver, the cells appear bounded by sinuous outlines that are often crenulated and lobed; as, for example, in the pulmonary capillaries of the frog and of mammals, in the capillary veins of the choroid of the rabbit, and in the capillaries of cephalopods. The dark contour lines often exhibit larger or smaller knot-like swellings. Many of these are composed of less deeply tinted substance, surrounded by the intensely brown cementing material, and perhaps consist of some modification of the latter, which is feebly acted on by nitrate of silver.

The slighter staining may, however, also depend on diminished thickness of the cement, whilst the deeper tints of other parts may proceed from the presence of particles of albumen, belonging to the original contents of the vessel, being retained in small indentations of the cell membrane, and becoming of a deep brown color by the action of the silver.

That the dark lines winding around the nuclei in the silvered wall of the vessel are not due merely to albuminous precipitates occurring in the small furrows surrounding the several cells, as Auerbach§§ appears willing to

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* Virchow's *Archiv*, Band xxxii., p. 172, 1865.

† *Archiv für Anatomie*, dated Jan. 18, 1865.

‡ Breslauer, *Zeitung*, Feb. 17, 1865.

§ *Sitzungsberichte der Physikal. Medicin. Gesellschaft zu Würzburg*, Feb. 18, 1865; *Medicinisches Centralblatt*, No. 13, 1865; *Uber den Bau und die Entwickelung der Blutcapillaren, Erste Abhandlung*, "On the Structure and Development of the Blood Capillaries, First treatise;" *Würzburger Naturwissenschaftliche Zeitschrift*, Band vi., 1866.

‖ *Medicinisches Centralblatt*, No. 14, 1865.

¶ Virchow's *Archiv*, Band xxxv., 1866.

** *Loc. cit.*, *Ueber die Capillaren der Wirbellosen*, "On the Capillaries of Invertebrate Animals."

†† Legros, *Note sur l'Epithelium des Vaisseaux Sanguins*, "Note on the Epithelium of the Bloodvessels," *Journal de l'Anatomie et de la Physiologie*, *Cinquième Année*, 1868, p. 275.

‡‡ *Sitzungsberichte der Wiener Akademie*, Band liii., 1866.

§§ *Virchow's Archiv*, Band xxxiii., 1865, p. 380.

admit, seems to be sufficiently refuted by the reactions of the cement in other membranes composed of cells, to which no application of nitrate of silver has been made. Besides the above-described dark intervening portions, clear areas of various size are also observable, interposed between the plexuses of lines. The margins of these are, for the most part, similarly dentated to those of the adjoining cells, but they are always of smaller size, and destitute of nuclei.

These appearances are not so frequently met with in the capillaries of mammals, but are common in the large arteries and veins, and also in the vessels of lower animals; as, for example, in the Cephalopods. Many of these non-nucleated areas (intercalated areas, as Auerbach calls them) may fairly be regarded as portions of the vascular cells which have been pinched off.

Small, irregularly shaped, dark, sharply defined spaces may, after treatment with nitrate of silver, be met with within as well as between the cells.

The number of the dark and clear intermediate areas varies much in different individuals, and more in the arteries and veins than in the capillaries.

Fig. 71.

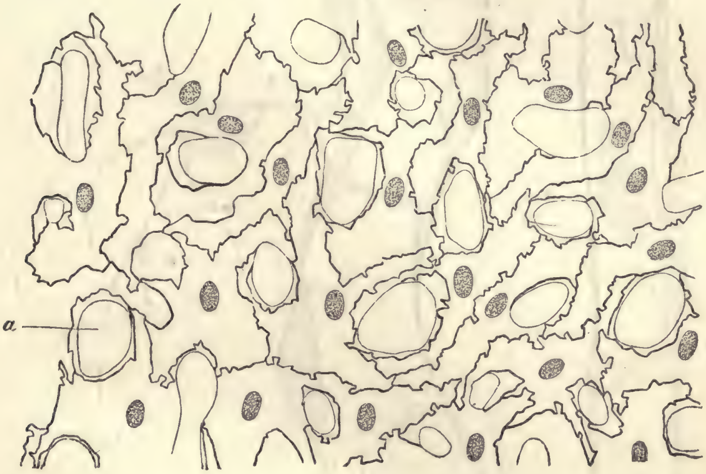

Fig. 71. Capillaries of the lungs of the Frog, with irregularly dentated cells. *a*, vascular meshes.

It has not been clearly proved that they are actually spaces in the wall (Stomata of Cohnheim). To enable us to understand the passage of blood corpuscles through the vascular walls, it is not requisite that coarse spaces or openings should exist, provided we may regard the vessel as composed, not of a stiff, but of a soft material, forming an elastic and permeable membrane. If the openings were really coarse, coloring particles of large size would pass through the vascular wall in various regions. But this never occurs. We do indeed see that fine coloring particles * escape through the vascular wall, but this does not occur easily with those possessing the diameter of the colorless blood corpuscles. These, on the other hand, by reason of their softness and elasticity, accommodate themselves to the fine in-

* W. Reitz, *Sitzungsberichte der Wiener Akademie*, Band lvii., 1868.

visible pores of the vascular membrane, and having traversed these, regain their original form.

Their escape must not, however, be regarded as a simply passive process, like the filtration of a colloid substance, to which it was likened in the first instance by Hering;* for it can be influenced in the most various modes by the contractility of the cells. Everything, in fact, which favors or checks their active motility influences their extravasation (Hering).

The finer capillaries consist only of a tube composed of cells or of a cylindrical layer of protoplasm. As the capillaries become larger, a delicate

Fig. 72.

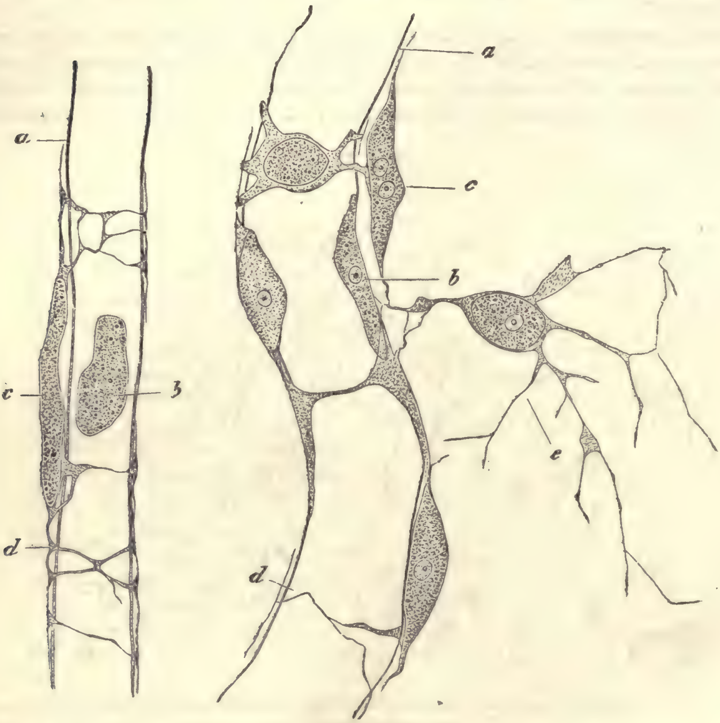

Fig. 72. Capillaries from the hyaloid membrane of the Frog. *a*, capillary wall; *b*, nucleus of the same; *c*, cells of the tunica adventitia; *d*, processes of these cells clasping the capillary wall; *e*, stellate cells anastomosing with the cells of the tunica adventitia.

tunica adventitia is superadded, which, in the hyaloid membrane of the frog (a membrane well adapted for this investigation), is formed, according to the researches of Iwanoff† and myself, of a delicate network of fine fibrils, composed of the processes of stellate cells lying directly upon the vascular wall. Each of these cells consists of a large elongated nucleus, invested by an extremely delicate layer of protoplasm.

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* *Wiener Sitzungsberichte*, Band lvii., 1868.
† *Medizinisches Centralblatt*, No. 9, 1868.

CHRONSCZCZEWSKY * observed, in capillaries which had been treated with nitrate of silver, the cells detached from their connections, and at the same time the external wall of the capillary prolonged over the hiatus. However little evidence there may be against the presence of a tunica adventitia in the capillaries of other organs, I must still remark that such observations as the above, for reasons that I cannot here discuss, are not always conclusive.

Fig. 73.

Fig. 73. A rather large capillary from the hyaloid of the Frog, presenting a membranous and nucleated tunica adventitia.

Between the capillaries of the hyaloid of the Frog isolated stellate cells occur, with round nuclei and delicate protoplasm, branching off into many processes which often anastomose with the processes of the cells of the tunica adventitia. Towards the small arteries and veins the pericapillary plexus becomes constantly closer, and soon in its stead there appears a delicate transversely folded and nucleated membrane, which is sometimes elevated in the form of small vesicles.

The general structure of these parts renders it scarcely probable that, as Iwanoff admits, the capillary sheath constitutes a lymph space.† Numerous examinations of the tunica adventitia of the larger hyaloid vessels, treated

* Virchow's *Archiv*, Band xv., p. 172, 1866.

† In my first treatise I described the capillaries of the pecten in the eye of the bird

with nitrate of silver, and undertaken with the view of detecting the indications of cells in it, have led, in all instances, only to negative results.

A similar nucleated membrane forms the outermost covering of the larger-sized capillaries, and of the arteries and veins of the brain, spinal cord, and retina of man. The action of nitrate of silver frequently brings into view irregular flat cells in their substance, which are often fused into one another. By careful treatment they may be obtained in the isolated condition. This layer may be distinguished as the *external vascular epithelium*, or still better, as the *vascular perithelium*.

The number of cells seen on a transverse section of a capillary tube is, with few exceptions, dependent less on their size than on their form, because the size of the cells *in the capillaries* corresponds with the calibre of the vessels. In the simplest examples, a fusiform spiral cell presents itself, the lateral surfaces of which are in contact, whilst the extremities occupy the spaces between the ends of adjoining cells. The capillaries in the pecten of the bird, even when extremely delicate, possess small polygonal cells, the breadth and length of which are nearly equal. It is only occasionally, and in the larger vessels especially, that the cells are distinctly fusiform.

As concerns the substance of which the cells are composed, it is always more abundantly and distinctly granular towards the centre and around the nucleus, whilst near the margin it is quite clear, and thins off to a delicate border. The capillary cells of the pecten of the bird, on the other hand, are, even in profile, only indistinctly fusiform, are of nearly equal thickness at the centre and at the margins, and consist of finely granular protoplasm, with a simple or divided nucleus, the contents of which frequently separate from the investing membrane of the nucleus, in the form of a roundish spherule, resembling a large nucleolus.

Only a few vascular regions form an exception to these statements; namely, the capillaries of the liver of Mammals and Amphibia, the chorio-capillaries of the former class, the hyaloid of frogs, and the young capillaries of the tadpole, and of pathological products of recent formation.

After repeated observations, I have only been able to discover the presence of cells in the capillaries in these instances, in a few isolated points; but in their stead I found fusiform or branched nucleated areas on the walls, bounded by finely punctated or interrupted lines. In the chorio-capillaris and the hyaloid membrane of the frog I found fusiform or polygonal cells in some only of the coarser capillaries, whilst in others no trace of them was discernible.

As regards the significance of these facts, three possibilities exist: either the capillary wall does not consist of cells at all, or, if this be the case, they have disappeared in consequence of fusion with one another, or the capillary wall has become only imperfectly differentiated into cells.

Now if, after repeated examination, a cellular structure is only demonstrable in the stronger and older capillaries, and but rarely in the younger, the conclusion is admissible, that all capillaries are not constructed alike, and that they are not altogether intercellular tubes. Supposing that a nucleated or a non-nucleated, and in the first instance solid process elevates itself from a capillary wall, gradually becomes elongated and hollow, its cavity commu-

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as possessing a delicate double-contoured tunica adventitia resembling the structureless membrane of certain gland tubes. More recently I have satisfied myself, from transverse sections of the pecten, that the apparent tunica adventitia is only the hyaloid membrane which invests the whole of the pecten, and from its exactly following the course of the vessels, gives, when seen on the flat, the illusory appearance of a complete tunica adventitia.

nicating with the lumen of the capillary—this may, in favorable cases, be regarded as a funnel-shaped outgrowth from a cell, but it is not an intercellular passage. In many instances, as in tadpoles, such outgrowths from capillaries are discoverable, which present no trace of cellular structure when treated with nitrate of silver, although in older vessels they can be readily brought into view. Must we not consequently conclude that the capillary wall thus beset with processes is similarly composed to the funnel-like projections, and that, as Stricker says, they are composed of protoplasm, which has assumed a tubular form?

The capillary wall is contractile both in young and in adult animals. Stricker* saw the capillaries not only of tadpoles, but of the nictitating membrane of frogs, contract to such an extent, that not even a single file of blood corpuscles could traverse them. Lastly, he observed small loop-like projections raise themselves from the wall of the capillaries of the nictitating membrane, and again become retracted. It is not improbable that it is by means of such contractions the corpuscles are pressed into the capillary wall, and ultimately made to traverse them.

Cavernous Vessels, Lacunar Blood Paths, Vascular Plexuses.

Cavernous vessels result from the unravelling of the vascular wall, which becomes converted into a spongy tissue; or from its becoming fibrous and membranous towards the lumen of the vessel, giving off processes that intercommunicate with each other, and which either form a spongy layer on the inner surface of the vascular wall, or a plexus traversing its entire calibre. A similar result is obtained from the occurrence of quickly consecutive anastomoses of vessels of various size. The primary vascular wall becomes teased out into thin trabeculæ and plates, varying in thickness, which are sometimes formed of simple cellular threads, and sometimes of all the tissues entering into its composition.

Structures of this kind are rarely met with in the arteries. The so-called carotid gland of the frog is, however, an example of it. In this instance, the strong muscular wall of the carotid artery forms internally a network of trabeculæ, enclosing spaces of variable size, which communicate freely with one another and with the lumen of the vessel. These trabeculæ are simple outgrowths of the vascular wall, containing muscle cells, which chiefly run in the oblique and longitudinal direction. I cannot corroborate the statement of Leydig, that these are transversely striated, but they are certainly much stronger than other muscles entering into the formation of vessels.

A similar structure has been found by Retzius to occur in the pulmonary arteries and aorta of the turtle.

The structure of cavernous veins consists, in some instances, of simple trabeculæ of connective tissue, as in the cavernous sinus, whilst in others it contains, in addition to the connective tissue, bloodvessels and muscular bundles running longitudinally, and anastomosing with one another, as in the corpora cavernosa of the generative organs. The endothelium of the vessels forms the innermost layer of these blood cavities.

The cavernous capillaries repeat, on a small scale, the relations of the cavernous veins. In the pulmonary organs of the snail the blood cavities are traversed by delicate nucleated trabeculæ, composed of fine homogeneous

* *Wiener Sitzungsberichte*, Bände li. and lii.

connective tissue. There is here as complete an absence of a cellular investment as in the great vessels of the lungs and heart.*

In the branchiæ of Crustacea the framework of the blood spaces is, on the contrary, composed of cells, the external expanded extremities of which rest immediately against the cuticle forming the so-called chitinogen layer, whilst the pyriform or clavate bodies of the cells which conceal the nucleus are applied to the axes of the gill laminæ, and adhere to the wall of the larger branchial vessels. Between the cells are roundish spaces intercommunicating with one another, through which the blood courses. There is no special membrane lining or limiting these blood passages.†

Fig. 74.

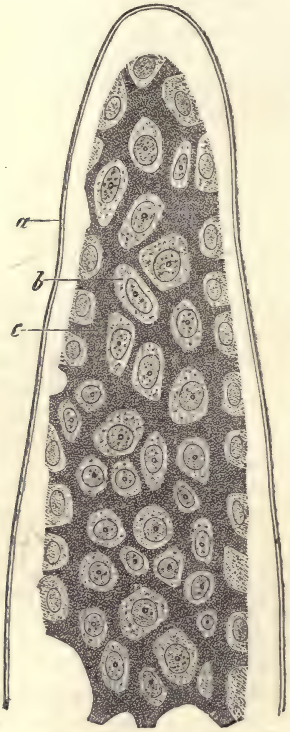

Fig. 74. Gill lamina of the River Crab. *a*, cuticula; *b*, clavate cells; *c*, lacunar passages for the blood in the interspaces of the cells. Surface view.

Cavities similar to these, through which the blood courses, are also found, according to Wilhelm Müller, in the spleen of mammals.

In the process of reparation of a wound there also originate finer or coarser intercellular blood paths, destitute of definite walls, which occupy the interspaces of the granulation cells. Originally they form an intermediary plexus of plasmatic canals which are supplied by the arteries,—the

* Semper, *Zeitschrift für wissenschaftliche Zoologie*, 1856. Eberth, *Blutgefässe der Wirbellosen*, "Bloodvessels of Invertebrates."

† Häckel, Müller's *Archiv*, 1857. Leydig, *Lehrbuch*, 1857, p. 385. Eberth, *loc. cit.*

blood issuing through spaces in the unravelled vascular wall, and being similarly discharged into the veins. A portion of these plasmatic canals subsequently expand into true bloodvessels, the walls of which are formed by the fusion of the cells lining the blood canals; the greater number, however, disappear altogether.*

Certain vascular plexuses are closely allied to the cavernous tissues, and, indeed, not unfrequently, as in the case of the papillæ of the comb of the cock, develop into actual cavernous spaces. Amongst these vascular plexuses there is one which lies in front of the coccyx in man, and deserves special notice, from the peculiarities of structure it presents, and to which it owes the names it has received from its discoverer, Luschka,† of coccygeal gland, and nervous gland.

This plexus forms a round or slightly oval, pale red, compact body, of at most 2·5 millimetres in diameter, the surface of which is either smooth or slightly tuberculated. Sometimes, instead of this single body, there may be found from three to six poppy or millet-seed sized masses, connected together by loose connective tissue, and seated on fine branches of the middle sacral artery. According to their discoverer, these bodies consist of fibrillar connective tissue, with numerous oblong nuclei, containing closed roundish vesicles, and simple or branched slightly varicose tubes, which are composed of a delicate structureless basement membrane, lined by an epithelium-like layer of round or slightly polygonal cells, replaced in recently born animals by true ciliated epithelium. The rich supply of nerves to these supposed glands, and especially of sympathetic fibres, and their position near the lower extremity of the great sympathetic, appears to justify the view that whilst the hypophysis is the cerebral pole of the sympathetic, this gland constitutes the anal pole, and is to be regarded as a nervous gland.

Luschka's statements, so far as regards the presence of gland vesicles and tubes, have recently been corroborated by Krause.‡—Arnold,§ however, calls the glandular structure of this organ in question, pointing out that the glandular bodies of the middle sacral arteries are capable of being injected, and that they only represent ampullar and fusiform dilatations of the lateral and terminal branches of that artery; in other words, a true plexus arteriosi coccygei.

These vascular sacculi, which may already be found as small, partial, but true aneurisms in the course of the middle sacral artery, and in larger number enter into the composition of the coccygeal gland, consist, according to Arnold, of an investment of connective tissue, which covers a layer of concentrically arranged and obliquely coursing muscular fibres, within which again is a delicate structureless coat, resembling the elastic fenestrated membrane. The innermost layer, the epithelial-like coat of the gland vesicles and tubes of Luschka, is composed of fusiform and polygonal cells, which frequently overlap each other at their edges. The connective intervening

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* Thiersch, *Artikel Wundheilung*, "Reparation of Wounds," in Pitha's and Billroth's *Handbuch der Chirurgie*, pp. 553 and 555.

† *Steissbeindrüse oder Nervendrüse des Beckens*, "Coccygeal Gland or Nervous Gland of the Pelvis," *Archiv für Pathologische Anatomie und Physiologie*, Band xviii., p. 106, 1860. *Der Hirnanhang und die Steissdrüse des Menschen*, "The Pituitary Body and Coccygeal Gland of Man." Berlin, 1860. *Anatomie des Menschlichens Beckens*, "Anatomy of the Human Pelvis." Tübingen, 1864, p. 187.

‡ *Zeitschrift für rationelle Medicin*, Band x., 3 R., p. 293. *Anatomische Untersuchungen*. Hannover, 1860, p. 98.

§ *Archiv für Pathologische Anatomie*, xxxii., p. 293, 1865; xxxv., p. 454, 1866; xxxix., p. 220, 1867.

substance of this is rich in muscles, which run in the most diverse directions, and form a continuous layer on the surface.

At a later period Arnold discovered the existence of similar structures, consisting partly of vascular sacs, and partly of retia mirabilia, in the course of the middle sacral artery in the dog, cat, otter, squirrel, rabbit, rat, horse, ox, and pig.

Krause and Meyer* have therefore corroborated the principal statements of Arnold, but, at the same time, have established the occurrence of a laminated epithelium lining the interior of the vascular sacs, and have pointed out the analogy of these with the carotid glands of the frog, and termed them caudal hearts.

Fig. 75

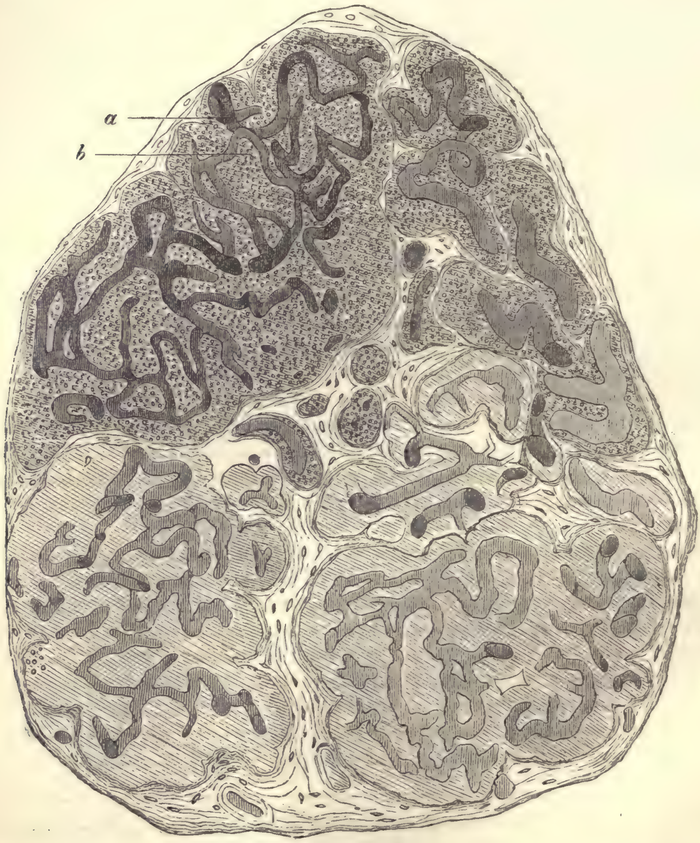

Fig. 75. Section of a naturally injected coccygeal gland. *a*, vessels; *b*, collection of cells.

The subject has again been taken up very recently by Sertoli,† and the results of his inquiries are not in accordance with those of the previous ob-

* *Zeitschrift für rationelle Medicin*, xxviii.

† *Archiv für Pathologische Anatomie*, Band xliii., p. 380.

servers. He finds that the stroma of the so-called coccygeal glands is formed of a tough, fibrous, richly nucleated connective tissue, traversed by bundles of smooth muscles, and containing rounded and elongated tubes, the walls of which are principally composed of fibres of connective tissue, running in a longitudinal direction, with, at most, a few isolated muscle cells distributed amongst them. These tubes become filled with polygonal cells, which, in concentric series of several layers, surround one or more centrally situated capillaries, or, less frequently, fine arteries or veins. These vessels are for the most part of normal calibre, and are rarely dilated; but when they are so, it is probably the result of manipulation.

My own view is that the coccygeal gland is a plexus of vessels which are

Fig. 76.

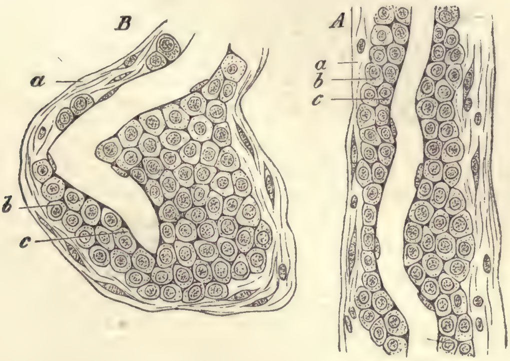

Fig. 76, A. Cellular vascular sheath, from the coccygeal plexus. *a*, connective tissue with scattered cells and nuclei; *b*, round and polygonal cells lying immediately upon the capillary wall *c*.

B. A capillary from the coccygeal plexus, with a vascular sheath very rich in cells. References as in A.

sometimes of equal width, and sometimes slightly dilated, or varicose, with lateral dilatations, which lie in a stroma of connective tissue, the numerous round, oval, and fusiform cells of which are certainly only in very small proportion muscular. The greater number of these vascular sacs are found in the capillaries and veins, and seldom in the arteries. Their number and size is often so considerable that true cavernous spaces are formed, and the intervening substance is reduced to a thin framework.

Around these vessels, and immediately external to their delicate cellular internal membrane, which is identical with that of the ordinary capillaries, lie rounded and elongated heaps of slightly polygonal cells, which are never invested by a definite structureless membrane, but have only a layer of connective tissue with longitudinal fibres on their outer surface. Many capillaries are invested, and frequently for considerable tracts, with a single layer of these cells, which are covered by a fibrous tunica adventitia containing numerous nuclei.

Small groups of similar cells lie also more remote from the vessels in the matrix or intervening substance. The larger cell masses must therefore be regarded as richer collections of these scattered through cellular vascular sheaths.

The size of these cell masses diminishes in proportion to the development of the vascular sacculi.

On one occasion I found in the cell masses laminated structures similar to those found in the granules of the thymus.

The intervascular tissue of the coccygeal gland is very rich in nerves. As regards the ganglion cells, which Luschka stated he had observed, neither Arnold, Krause, nor myself have been able to satisfy ourselves of their presence. Nor have I been more fortunate in obtaining a view of the club-shaped terminations of the nerves resembling Pacini's corpuscles, or terminal bulbs, described by Luschka. They are said to be 0·8 millimetres broad, and to possess a thick membranous and fibrous investing sheath containing numerous longitudinal nuclei.

Inasmuch as a glandular structure is not demonstrable in the so-called coccygeal gland, which rather appears to consist of a rich plexus of for the most part capillary vessels, invested by a cellular sheath, some of which are normal, whilst others are dilated in a fusiform or sacciform manner, it is clear that for the future it should be named the plexus vasculosus coccygeus, and that it should be classed with the carotidean vascular plexus of the so-called carotid gland, at the upper extremity of the common carotid of man and mammals.

CHAPTER IX.

THE LYMPHATIC SYSTEM.

By PROFESSOR F. v. RECKLINGHAUSEN.

In consequence of the pressure under which the blood courses through the vessels of the several organs of the body, the tissues are constantly permeated with serous fluid, which partly furnishes the materials requisite for their nutrition, and is in part also subservient to the preparation of the secretions. This serous or tissue fluid requires constant renewal, a rapid exchange of material, without which it quickly alters the composition of the various tissue elements around which it plays. The passage of fresh fluid from the blood into the tissues would, however, cease as soon as the pressure of the latter approximated that under which the blood moves in the vessels, were not a constant escape of the fluid provided for by means of a canal system, which is so far separate from the bloodvessels supplying the tissues, that the pressure of the blood is not transmitted directly into the canal system—that is to say, not with its full force. These canals, the lymph vessels, form therefore a peculiar system, the rootlets of which are distributed through the tissues, and which only so far stands in connection with the bloodvessels, that it, 1st, indirectly withdraws from them the fluid they contain, and, 2d, that it ultimately returns that fluid to the bloodvessels by its terminal trunks. The origin of the lymphatic system is in relation with the capillary vessels in which the blood moves under a considerable pressure; its termination, on the other hand, communicates with the chief venous trunks, and consequently with those parts of the vascular system in which the blood pressure descends to its minimum amount, and is in fact almost reduced to zero.

The difference in the amount of these two pressures constitutes an essential factor in the production of the movement of the lymph; so that the greater the difference, the more rapid is the movement. The lymphatic vascular system borrows its contents, as well as the impulsive force under which they move, from the blood vascular system; and in so far it may be regarded as an appendage of, or as an accessory closed system to, the blood vascular apparatus.

The dependency of the lymphatic system on the bloodvessels is indicated by the circumstance that, as a general rule, the lymphatic system in any organ is so much the more strongly developed in proportion as its supply of bloodvessels (mucous and serous membranes, skin, glands) is more abundant; but there are also organs characterized by a peculiar richness in lymphatic vessels, which are at the same time especially adapted for absorption (gastric and intestinal mucous membrane, central tendon of the diaphragm).

The entire lymphatic system may be divided into two sections; the first containing the fluid which, immediately after its escape from the bloodvessels, circulates around the several elements of the organs, the interstitial serous spaces; and, secondly, the system of the efferent canals, the proper lymphatic vessels. This second section will be here first described, because its structure is much more accurately known.

The efferent canals, or *lymphatic vessels*, ordinarily agree in their form, arrangement, and in the structure of their walls with the bloodvessels. In the greater number of organs they form plexuses, which are so much the more close, the more abundantly the tissues are supplied with bloodvessels: moreover, they only occur in association with bloodvessels; and those tissues which are destitute of bloodvessels, like the cornea, vitreous humor, and epithelial tissues, possess also no proper lymphatics. Like the bloodvessels, they generally form cylindrical tubes, and only in certain regions, hereafter to be described, present the characters of fissures or lacunæ, under which condition, however, they not unfrequently form investing sheaths for different organs. The lymph vessels may be distinguished for the purposes of description into the smallest branches, the capillaries which are intercalated between the system of the blood capillaries, and the larger lymph vessels which issue from the several organs, and ultimately unite to form the main trunks.

The *larger lymphatics* of Mammals and Birds are always tubes, the walls of which agree with those of the bloodvessels in their structure, and hence present a tunica intima very rich in elastic fibres, and lined by a single layer of tesselated epithelium: a tunica media, consisting exclusively of muscular elements; and a tunica adventitia, composed as usual of loose connective tissue. The tunica media does not attain the thickness of that in the arteries, but its fibres pursue a similar transverse direction. Upon the whole, the lymphatics are not so thick-walled as the arteries, but, in the relation between the thickness of the wall and the calibre of the vessel, assimilate much more closely to the veins. The form of the lymphatics of Birds and Mammals is peculiar, and so far differs from that of the bloodvessels, that they are provided with very numerous valves, resembling generally the valves of the veins. Immediately above each valve the vessel is somewhat wider than just below, and not unfrequently there is a distinct saccular dilatation at this point. As a consequence of this arrangement, the lymphatics only preserve their cylindrical form for short distances in those parts which are destitute of valves, whilst in those parts where the valves are numerous they assume a varicose or moniliform appearance. The valves, like those of the veins, are simply duplicatures of the tunica intima.

The structure and arrangement of the larger lymphatics present essentially different features in the Amphibia. They do not here form even approximatively cylindrical tubes, but *lacunæ*, which occupy the interspaces between the several organs. If, in consequence of an arrest of the flow of the lymph, or by artificial injection, they become more completely filled than is natural to them, they swell out in the form of large sacs, which, however, possess no constant or definite form, since they only represent interstitial spaces. As a general rule they do not possess an independent thick wall, capable of being detached from the surrounding parts, but their limits or boundaries are formed by the fasciæ and such condensed layers of connective tissue as are found on the surface of the different organs, the surface which is turned towards the interior of the cavity being covered with a single layer of tesselated epithelium. Only such septa as divide the several lymph spaces from each other, and are composed of pure connective tissue, can be regarded as properly belonging to them. The lymph sacs in these animals therefore resemble the peritoneal and pleural sacs, with this difference, that the lymph sacs communicate with one another by means of microscopic openings in their septa, and consequently form a continuous system of cavities. Inasmuch as the lymph sacs are almost entirely destitute of proper walls, the muscular elements, the function of which is to aid in the propulsion of

the lymph, also fail; but in their stead special contractile organs, acting rhythmically, appear in certain parts of the lymphatic system of Amphibia. These constitute the lymph hearts discovered by J. Müller, and one of them lying posteriorly near the sacrum propels the lymph into the sciatic vein, whilst the anterior pumps it into a branch of the jugular. They are chiefly composed of transversely striated short muscular laminæ.

These peculiarities in the structure and arrangement of the large lymphatics of Amphibia, in contrast with those of other Vertebrata, are of great interest. They prove clearly that great variability occurs in the lymphatic system, much greater even than in the blood vascular system; and, in truth, this variability occurs not only in different classes of animals, but in one and the same species, and not only in the larger trunks, but in the smaller vessels. The number and size of the principal trunks of any organ, as, for example, of one of the extremities of man, presents as little constancy as the mode of their division. Even in one and the same organ the results of injection are often quite different, and it frequently happens that injections of the same organs in nearly allied animals present such remarkable differences that only the most general statements can be made in reference to the arrangement of the lymphatics of any particular locality.* It is obvious, therefore, that those typical modes of arrangement which occur in the arterial and capillary blood vascular systems of the different organs can only be imperfectly demonstrated in the lymphatics, and that only the general relations existing between the structure of any organ and its lymphatics present characteristic features. The varieties that occur in the arrangement of the lymphatics exhibit many peculiarities in certain regions of the smaller lymph vessels. Thus we see, in parts where they are very numerous and closely arranged, there are not unfrequently lacunar spaces even in Mammals, as if they had coalesced to form a flat and wide vessel; we meet also with a pair of lymph tubes accompanying a bloodvessel, and not unfrequently with regular sheaths, which partially or entirely surround them, as, for example, in the case of the chyle vessels in the mesentery of the Mouse (Brücke). In such instances as these we recognize in Mammals arrangements essentially similar to the lymph sacs of Amphibia.

There is still another circumstance that becomes intelligible from this comparison if we remember that certain sections of the lymphatic system of the Amphibia do not possess a tubular form, but represent ensheathing or lacunar spaces. They are thus analogous, as we have already seen, to serous sacs, and it will be understood how the latter stand in immediate relation with the lymphatic system, are in direct communication with it, and possess similar contents (see *infra*).

This variability of form recurs in the narrowest section of the lymphatic system, that is to say, in the *lymphatic capillaries*. For even among Mammals we meet in certain organs with lacunæ, representing the roots of the lymphatics; whilst in Amphibia the great majority of the lymph capillaries are tubular. The lacunæ correspond in form with the spaces between the parts of the organs they invest, such as the ducts of glands, etc. The capillary tubes, even in their finest branches, are provided with varicose enlargements, and these are often situated at the points of junction of the vessels, and occur so suddenly that transverse processes project into the lumen of the vessel, which are again so placed that they form a kind of valve. Such dilatations often succeed one another at very short intervals, especially in those lymphatics which immediately follow the capillaries, giving the impression of

* See the illustrations in L. Teichmann's *Saugadersystem.* Leipzig, 1861.

tubes constructed of a series of Florence flasks, of which each is inserted by its neck into the base of the one preceding it (see fig. 77). It is easy to recognize, from the position of these processes, what direction the lymph current pursues in any particular vessel, since they are so arranged that, like the valves of the larger lymph vessels, they prevent any regurgitation of the fluid.

The arrangement of the capillary lymphatics in reference to the blood-vessels is a subject of special interest. The larger lymphatics run sometimes in immediate proximity to the arteries and veins, and sometimes separately, or, at all events, present no constant relation to them. But for the smaller and capillary lymphatics, the general statement may be made that they hold their course at as great a distance as possible from the blood capillaries. This characteristic feature may be most easily recognized in membranous expansions, in which the blood and lymphatic capillaries are distributed upon one plane: in such cases the points of junction of the lymphatic plexus always occupy the middle points of the meshes of the blood capillaries, and the converse. It is evident that this arrangement is most advantageous for the purpose of drainage. All fluid escaping from the blood capillaries must traverse the tissue to reach the capillaries; and so long as this transudation occurs, a continuous play of fluid around all the tissues must take place. If, on the other hand, the lymphatic efferent canals lay in immediate contiguity to the blood capillaries; if the whole were not, so to speak, intercalated between the tubes of the lymphatic system and of the bloodvessels, the fluids might easily stagnate in those parts which were more remote from both, and a constant interchange of material would cease to take place. There is yet another point that is deserving of notice. In those membranes which present a free surface covered with an epithelium, as in the mucous and serous membranes and the skin, the lymph capillaries are found constantly to occupy a deeper plane than the bloodvessels. Whilst the latter ascend till they lie just beneath the epithelium, the lymphatic capillaries do not reach the uppermost stratum of connective tissue. These relations are most easily recognized in the membrane forming the web of the foot in the Frog, which is a duplication of the external skin; the lymphatics here exclusively lie in the middle connective tissue layer, whilst the bloodvessels course in the thin cutaneous laminæ on either side. A similar arrangement of the two sets of vessels is strikingly shown in the case of the villi of the small intestine, in which the proper tissue of the villi forms a peripheric layer traversed by a close net-work of capillary bloodvessels, whilst the chyle vessel lies quite in the interior, near the axis, and is generally single and unbranched, as in the rabbit, ox, sheep, and man, though occasionally it has been observed to form a set of anastomosing capillaries, as in the dog, sheep, and ox. Again, if the results obtained from the injection of the cutaneous lymphatics by Teichmann, in a case of elephantiasis,* be considered to represent the normal distribution of the lymphatics, the capillaries of this system lie exactly in the centre of the papillæ of the cutis, whilst the blood capillaries traverse their periphery.

At first sight it appears remarkable that the lymphatics should lie so deeply in organs destined for absorption, as, for example, in the villi; this relation, however, is in itself a sufficient indication that the connective and other tissues of the villi play a most important part in the act of intestinal absorption, and that here also the central chyle vessel only acts as an efferent or drainage pipe. The function performed by the roots of plants is probably

* *Untersuchungen über das Saugadersystem*, Taf. 6, fig. 4.

similar to that of the epithelium and the parenchyma of the villi. The chyle vessels, on the other hand, appear to be analogous to the vessels and fibrovascular tissue of the plant; if these were able to absorb, a more superficial position would be more appropriate to the discharge of their function.

Having now learnt the form and arrangement of the capillary lymphatics, we turn to the consideration of their structure, a question which has recently received particular attention, and has met with various answers. Are they,

Fig. 77.

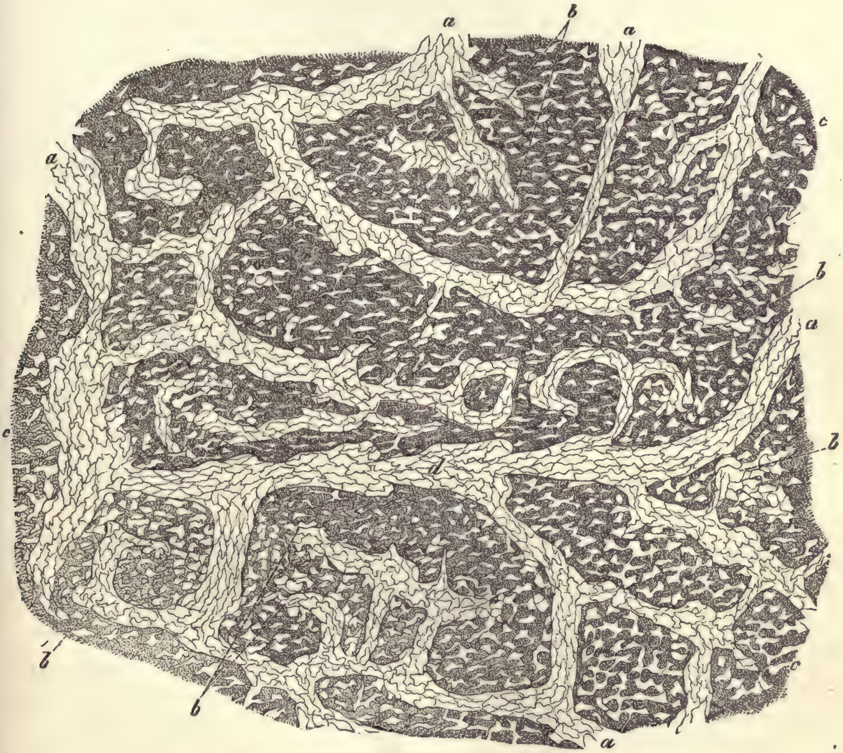

Fig. 77. Central tendon of the diaphragm of a Rabbit, treated with silver, and examined from the thoracic side. *a*, lymphatic capillaries with the contours of the epithelial cells; *b*, first appearance of the cells; *c*, connective tissue with serous canals; *d*, flask-shaped dilatations. Magnified 60 diameters.

like the bloodvessels, provided with a proper wall, or are they destitute of a limiting membrane, constituting only lacunæ, or spaces in the tissues amongst which they lie? The decision of this question is particularly interesting in the case of the chyle vessels of the villi. The chyle formed after the ingestion of food, containing abundance of fat, owes its white color to the presence of numerons extremely fine molecules, which are probably oil globules. Particles of a similar nature are met with during the process of absorption, both in the parenchyma of the villi and in the epithelial cells. In all probability, therefore, they press through the epithelial layer as un-

dissolved molecules into the substance of the villi, and beyond this into the central lacteal. It would hence appear that the paths traversed by these minute oil drops in the periphery of the villi open directly into the central chyle vessel; and the simplest view is, that no special limiting membrane exists (Brücke). On the other hand, microscopic examination shows that there is really a double, and not a mere single, outline to be seen in the central lacteal and in the finest capillaries in the tail of the Tadpole, from which the conclusion has been drawn that a homogeneous investing membrane is present (Kölliker). It was found also that in injected preparations the injection tightly filled the capillaries of the chyle and lymphatic vessels, without the escape of any of it into the surrounding tissues; and hence it was considered that the assumption was perfectly justified, that these vessels were as completely enclosed by an investing membrane as the bloodvessels themselves (Teichmann, Frey). In point of fact, the presence of a special membrane in the lacteals and lymphatics may be most easily proved by the application of the silver method of staining the tissues adopted by Recklinghausen. If a solution of silver be injected into the lymphatics as far as the capillaries, or if the tissues be generally impregnated with a solution of this salt, fine dark lines appear in the lymphatic capillaries (fig. 77), which are usually strongly looped or sinuous, including polygonal, or not unfrequently rhombic, areas, in all their peculiarities identical with the silvered lines of the most various epithelial tissues. The networks of silvered lines become visible as early as in the rather larger vessels succeeding the capillaries, where the enclosed areas are fusiform, and agree with those brought into view by the agency of silver on the inner surface of the large lymph and blood vessels. In the case of these last-named vessels, it may easily be proved that the lines in question depend on the presence of a single layer of flat epithelial cells lining the tunica intima; but, inasmuch as the same markings may be traced continuously into the lymphatic capillaries, it follows that these also possess a similar layer of tesselated epithelium.

In fact, even in the capillary lymphatics, subseqeunt treatment with carmine not unfrequently brings into view an oval nucleus in each area. Moreover, if the intestinal villi be torn off a few hours after death, we may sometimes meet with one from the centre of which a wide tube projects, consisting of flattened epithelial cells.

It is no longer, therefore, a matter of doubt that the *capillary lymphatics* —at least, in those organs in which they have been investigated with special reference to this point, as the serous membranes, the walls of the intestine, the diaphragm, both in its muscular and tendinous portion, and the membrana nictitans of the Frog—*are lined by a single layer of flattened epithelium.* They also possess a special membrane, though not completely homogeneous and structureless, as was formerly maintained, nor entirely closed, as we shall hereafter have occasion to see.

I was formerly of opinion, after I had satisfied myself of the presence of an epithelium in the lymphatic capillaries, that I had by this means discovered an essential distinction between them and the blood capillaries; but, as subsequently it has been shown by experiments with silver that the wall of the capillary bloodvessels, in some organs at least, consists of epithelial cells, the distinction fails.

The lymphatic capillaries are, in fact, constructed on the same type as the blood capillaries (see the section on the bloodvessels). The existence of such an analogy has been contested, because the blood capillaries can be easily isolated in portions of considerable length in some organs, as the brain, whilst it is very difficult to exhibit such detached portions of the capillary walls of the lymphatics. Very recently Frey has

been led to the conclusion * that, "whilst in the blood capillaries the walls maintain a perfect independence in regard to surrounding tissues, in the lymphatics they fuse with them." I believe that we must beware of admitting that the blood capillaries are so completely isolable in all organs, or form such independent tubes, as in the brain. In many glands—as the liver, for example, not to mention the spleen—the wall of the capillary bloodvessels is not capable of being isolated.

And now arises the question, do the lymphatic capillaries possess a special wall or not? Admitting an answer in the affirmative, are the above-mentioned phenomena taking place in the resorption of chyle consonant with it? They would appear to demand that the lumen of the chyle capillaries should not be closed towards the free surface of the mucous membrane. But these appearances can be equally well explained, if we suppose that the wall is not everywhere formed of a continuous solid layer, or, in other words, that it possesses foramina. Up to a recent period it has been generally accepted that epithelial investments, except in the case of glandular epithelium, serve as a protection to the subjacent tissues, and therefore, by the intimate union of the cells with each other, form a firm, close tissue, permeable only for fluids. Since, however, the terminal apparatus of the sensory nerves has been discovered in the epithelial strata, and very recently also cup-shaped organs, both of which seem to be but ill adapted for protection, the epithelial tissues have gradually attracted more and more attention from histologists, and it is not surprising that further inquiries should be undertaken with the view of discovering other and peculiar arrangements. It is reasonable, therefore, on *à priori* grounds, to concede that the epithelial coating of chyle and lymphatic capillaries may present special peculiarities which stand in relation to the absorption of material from the surrounding tissues, and may, at any rate, at certain times, facilitate their passage. In some lymphatics, openings of appreciable size are already known to occur, through which, even during life, small bodies may be absorbed into the interior of the tube. They were first demonstrated by Recklinghausen, in the central tendon of the diaphragm. If we inject into the peritoneal cavity of mammals milk, blood, or fluids which have insoluble substances (consequently not carmine) in suspension, a beautiful injection of the net-work of lymphatics of the central tendon of the diaphragm may be obtained. If we press a cork ring against the central tendon from the thoracic side, attach a portion to it with needles, and then excise it, we are enabled to procure the surface of the tendon in an absolutely uninjured state. If now we place a drop of milk upon this, the absorption of milk globules into the lymphatic vessels may be directly observed under the microscope. The milk globules run towards certain points at which small vortices occur whilst they are penetrating into the subjacent lymphatics. The openings through which they gain entrance are only wide enough to admit two or three milk globules abreast, are roundish, sometimes even quite round, and represent, as is clearly shown by subsequent staining with nitrate of silver, spaces between the epithelial cells. They usually lead perpendicularly into the lymphatic vessels, over which they are immediately placed, but sometimes they are situated somewhat obliquely, towards the margin of the vessel, or they may even be as far distant as a semi-diameter of the vessel, in which case there is an oblique canal leading to the latter.

The openings (stomata) never exceed the size of an epithelial cell. The rich lymphatic plexus of the central tendon with these large stomata is obviously subservient to the absorption of the fluids of the peritoneal cavity,

* *Handbuch*, p. 427.

which, like the lymph, contains contractile cells, capable, from their size, of passing through the stomata. In the frog, which has no diaphragm, Schweigger-Seidel and Dogiel found that openings of a similar nature exist in that surface of the wall of the cisterna lymphatica magna that is turned towards the abdominal cavity. Dybskowsky also was able, by causing the absorption of colored fluids from the pleural cavity of dogs into the lymphatic plexus of the pleura, to demonstrate the existence of similar openings between the epithelial cells. From these experiments we may now reasonably expect that analogous formations will be found in the pericardium and in the arachnoid membrane of the brain, and that, consequently, we may conclude all serous cavities to possess a very intimate connection with the lymphatic system.

Further, it has been shown, in regard to many epithelial layers, even in parts where the lymphatics certainly do not approximate the surface, that when they have been treated with nitrate of silver, sharply defined spaces exist between the epithelial cells which may be placed in the same category with the stomata above described. Oedmansson first described them in the epithelia of serous membranes. He drew attention to their occurrence in the epithelial stratum of the chyle vessels and of the follicles of Peyer; Ludwig, Schweigger-Seidel, and Dybskowsky demonstrated their presence in the pleura and peritoneum, and further showed that they were especially abundant in the small-celled epithelium which lies directly over the lymph vessels on the peritoneal surface of the central tendon of the diaphragm. They are distinguished from the proper stomata by their much smaller size, the largest only attaining the diameter of a red blood corpuscle, and they are principally found at the points of junction of several epithelial cells. I recognized these spaces when I first began to employ silver as a means of staining the tissues; but have met with them under so many different conditions, that I am not at present satisfied of their nature. In perfectly fresh silvered preparations, preserved as carefully as possible in their natural condition, we frequently meet with areas of considerable extent in which scarcely any openings are present, whilst in others, again, they are very numerous; the difference being in no way attributable to the mode of preparation. At the same time, it cannot be denied that within a few hours after death, or as a consequence of mechanical violence, or careless preparation, they always appear more numerous, clearly on account of the epithelial cells becoming detached from each other. The variability in the appearances presented by perfectly fresh specimens may be explained on the supposition that at certain times, or under certain conditions, connected with the imbibition of fluids, the substratum of the epithelium opens, whilst under other conditions it closes up. At present no absolute proof has been adduced to show that they are really openings, nor has any one shown that solid particles can traverse them.

I must express myself in exactly the same terms in regard to the very regular and interesting appearances of a similar nature, situated for the most part at the points of junction of several epithelial cells, which are frequently exhibited in the lymph vessels of silvered preparations, but which are sometimes undiscoverable even when the greatest care has been taken in the preparation of the specimen. I endeavored to obtain them constantly, and hoped, in accordance with what has been above stated, to accomplish this by permitting the central tendon to lie for several hours in diluted pericardial fluid, thus rendering its tissues as moist as possible with an indifferent fluid, yet without being able to observe the spaces occur with such constancy and regularity as, after the foregoing exposition and the observations I have still to make, was to be desired. The present condition of our

knowledge may therefore be expressed in these terms: that stomata can be certainly proved to exist in certain lymphatic capillaries; that openings, at least of an occasional character, must also exist in other lymphatics, especially in absorbing membranes, though this still remains to be satisfactorily demonstrated, notwithstanding that Oedmansson, His, and others have described foramina presenting features analogous to such stomata.

We come now to the essential point of the whole inquiry, the nature, namely, of *the relation borne by the lymphatics to the surrounding tissues.* And we must first ask whether definite channels exist by which the fluids transuded from the blood are conducted to the commencement of the lymphatics, or whether the surrounding tissues behave like Descemet's membrane, in which pores and canals are present of sufficient magnitude to enable them to be readily seen by means of the microscope? If we consider the phenomena of the absorption of fat, it appears absolutely requisite to assume, not only that there are foramina in the walls of the capillary lymphatics, but that there are channels in the surrounding substance of the parenchyma in the case of the villi, though in regard to other rootlets of the lymphatic vessels, their existence appears less requisite, since their contents, apart from the lymph corpuscles which are probably formed in their interior, ordinarily consist of a fluid destitute of any undissolved particles, or oil drops. In the parenchyma of the villi, a plexiform disposition of the chyle constituents has been observed to be situated immediately beneath the epithelium, forcibly suggesting that special arrangements are here present, by means of which the vessels containing the chyle are brought into direct communication with the cavity of the intestine. Very recently it has been maintained by Letzerich that a special system of canals, commencing with cup-shaped organs, in the epithelium, conducts the chyle into the central lacteal; but, even in the event of this statement proving correct, there must still be apertures or canals analogous to those above described, which lead from the abdominal cavity to the lymphatic vessels of the central tendon of the diaphragm.

A lively discussion is still maintained as to whether the lymphatics are closed channels, or whether they stand in communication with interspaces of the tissue, from which, indeed, they may be supposed to be developed. The former view has become more definite since Virchow and Donders advanced their doctrines respecting the stellate connective tissue corpuscles; the corpuscles, in consequence of the fusion of their membranes, are supposed to form a continuous system of tubes, a plasmatic vascular system, or, as it was called by Kölliker, a system of serous tubules, easily suggesting what was said in precise terms by Leydig, that this system of tubules was intercalated between the blood capillaries on the one hand, and the lymphatic capillaries on the other, and constituted the direct path between them. This statement was mainly supported by observations made on the tail of the tadpole, in which Kölliker found a distribution of lymphatic vessels with dentated outlines in connection with stellate, angular bodies, the connective tissue corpuscles. Whilst all such stellate and angular bodies require the existence of a membrane to be admitted, both this plasmatic system and the lymphatic system were regarded as closed. Physiologists, however, and particularly Brücke and Ludwig, maintained the view that the roots of the lymphatics, themselves destitute of a membrane, commenced simply from the interstices of the tissues, or from the so-called lacunæ. Fohmann, and before him Mascagni, had already, by injecting the lymphatics with mercury, obtained, when sufficient pressure was employed, such complete injections as to arrive at the conclusion that the tissues were entirely composed of a close plexus of lymphatics, and that the solid tissues con-

stituted only small trabeculæ and septa between them. Brücke, in support of this view, argues from the known fact "that when injections of the bloodvessels are performed shortly after death, and therefore whilst the fluids permeating the tissues, as the lymph and blood, still remain uncoagulated, in not a few cases either the entire mass of injection, or the fluid portion of it, returns by the lymphatic vessels, which thus become even more completely filled than can be effected after the employment of much care and trouble." Ludwig and Tomsa have, moreover, in their injections, driven gelatinous fluids into the ultimate lymph canals of the testes in man and in dogs, and the injection was found to fill almost all the intervals between the tubuli seminiferi, following their course, and thus occupying spaces which form continuous lacuniform sheaths around the ducts. The contiguous lacunæ were divided from one another by very thin septa of connective tissue, in which the bloodvessels ran. On a small scale, therefore, the arrangements were similar to those met with in the lymph sacs of Amphibia. The idea was consequently not far fetched, that these appearances originated from the manipulation of the specimen, and the extravasation of the fluid; and, in fact, this objection was raised by the opponents of the view held by Brücke and Ludwig; and Langer even pointed out that in the testes of the frog the lymphatic vessels do not form sheaths of this nature, but tubular plexuses, as is usual in the lymphatic capillaries of other parts. Nevertheless it cannot be doubted that in the testes of many Mammals the lymphatic tubes ultimately terminate in lacunar channels. Ludwig and Tomsa have further attempted to prove the existence of such interstitial lacunæ in other organs, as in the tongue and kidneys, and to demonstrate their connection with the lymphatic vessels.

From this exposition of the two opposite views, it is obvious that they differ from one another in one point, which is deserving of especial notice. In the one view, the anastomosing connective tissue corpuscles form a plexus, the nodal points of which are represented by the body of each corpuscle; the fibres of the plexus are *hollow cylinders*, and their disposition, upon the whole, similar to that of the lymphatics. On the other view, the interstitial spaces depend for their form on that of the morphological elements of the tissues (ducts, fibres, etc.) between which they lie. They vary in their form and size, but in general, because by far the greater number of tissues consist of cylindrical or spherical elements with more or less convex surfaces, they constitute *fissures* (that is to say, spaces the transverse section of which is not circular, as in tubes, but elongated, presenting in some instances a very small, and in others a relatively large diameter). Special importance has been attached to this lacuniform character of the channels by Ludwig. At the point of transition of these into the proper lymphatics, the lymph path undergoes a sudden alteration of form.

In opposition to these two views, I have still a third to propose, which is in accordance with all the facts that have hitherto been observed. The essential feature of this is, that the masses of connective tissue, whether they form the exclusive structure of an organ, or are intercalated between the proper morphological elements of some other tissue, are traversed by fine canals, the *serous canaliculi*, which are directly continuous with the lymphatic vessels. These canals, in many organs, form plexuses, so that portions of them appear to be branched in a stellate manner exactly resembling the connective tissue corpuscles. These last, however, are not, as Virchow, Kölliker, Leydig supposed, fused with the walls of the lymphatic vessels, but occupy the interior of the serous canaliculi, so that from this point they may extend into the lumen of the lymphatic vessels. Moreover,

the serous canaliculi are not provided with a special wall, and are consequently not tubes, on which account they are to be distinguished from the serous canals of Kölliker, but are rather to be regarded as excavations in the remaining substance of the connective tissue. They do not, however, represent—and on this account my view is to be distinguished from that of Brücke and Ludwig—mere fissures between the specific components of the connective tissue, but are the interstices of the fibrous fasciculi and lamellæ of connective tissue, cemented to one another by a tenacious homogeneous firm material in which the serous canaliculi are buried. Their form and arrangement, whilst it is not independent of the form of the interstices, is yet not altogether identical with it, but peculiar, and one not entirely determined by the arrrangement of the several morphological elements of the organ. On my view, therefore, it cannot be admitted that the commencement of the lymphatics are, as Ludwig imagines, simply lacunæ, whilst, on the other hand, it is equally opposed to the view that they constitute closed membranous tubes, as is maintained by the adherents of the doctrine that they owe their origin to the connective tissue corpuscles.

When organs composed of connective tissue, and recently removed from the body, are treated with solution of nitrate of silver, the solid parts alone become stained, whilst spaces and channels in the tissue remain uncolored; the lymph and bloodvessels coming into sharp relief as colorless tracks. In the connective tissue itself, stellate, unstained figures make their appearance, which are consequently spaces, though not altogether empty, since, by this mode of treatment, connective tissue cells become dimly visible in their interior. His maintained that the silvered tracings of the cornea agree with the form of the cells; in other words, that the solid substance presents cavities which precisely correspond to the cells and their processes. In the mean while, if we allow the corpuscles of the cornea, with all their processes, to come into strong relief, by exposure for several hours in the moist chamber (which is the best method of rendering them distinct), the ramifications of their processes are always found to be few in number, and the communications between their finest branches to be discovered only with difficulty, whilst the silvered lines form a close plexus; the stellate corpuscles of the cornea, however, do not become covered with the tracings. But further, we see the actively moving cells of the cornea traverse its substance in all directions, without, as a rule, attaching themselves to the processes of the stellate, immovable corneal corpuscles, though they sometimes do so with great distinctness; with the spaces in which the latter lie, channels must therefore still be in communication, which are not occupied by the protoplasm of the cells. Moreover, W. Engelmann, since the migrations take place in every possible direction, has drawn the conclusion that the cells run without obstruction between the fibrils of connective tissue, pressing in from one to the other; various circumstances, however, are in opposition to this view. By careful observation it may be seen that the movements of the migrating cells do not take place with equal facility in all directions. They become constricted at certain points, and these constrictions remain unaltered in position, whilst the several corpuscles force themselves through; again they appear to meet with an obstacle, and must pass round it, though the constricting and obstructing substance may be so delicate as not to be visible. But further, if the cornea, or other variety of connective tissue (independently of the cells) consists only of fibrils with intervening fluid, in cases where the injection of an insoluble mass has been effected by means of simple penetration, the whole tissue can be split up into fibrils, or, in the case of the cornea, into lamellæ, and we may then ob-

tain the sub-cylindrical canals (Bowman's corneal tubes), which often form very distinct plexuses. It is true that the latter, as they appear after injection, present a very unnatural form, being dilated to an enormous extent, on which account, however, they must not be at once cast aside as "artificial products," but they rather show, since their forms cannot be referred to the arrangement of the fibrils, that the interfibrillar and interlamellar substance does not possess, in all directions, an equal density, but must consist of a soft fluid mass, and a firmer and more resistant material. From microscopical investigation we learn that the corneal corpuscles are situated in the channels which contain the injection; this must consequently correspond with their natural position, and it follows that these spaces are, at least in certain directions, immensely dilatable, and can scarcely therefore possess a proper investing membrane. If we take all these facts into consideration, we must, I think, come unavoidably to the conclusion, first, that, in the denser organs composed of connective tissue, as the cornea, tendons, fasciæ, and cutis, the lacunæ between the fibres or fasciculi are not filled with fluid alone, but in great part contain a more solid cementing substance; and, secondly, that in this more solid substance there are no cavities constituting matrices for cells, although plexiform canals destitute of walls are present, which are partly filled with cells, and partly with a variable quantity of fluid consisting of the juice of the tissues.

Since the nitrate of silver, when properly applied, only colors the solid tissues, the serous canals appear as colorless bands, resembling the lymph and blood vessels, which can be followed to their finest branches with a facility proportionate to their breadth, or as they happen to be filled more strongly with fluid at the time when they were stained with the silver. We must attribute the incomplete appearance of the plexuses in some cases to the absence of fluid, especially where the wider parts only, in which the connective tissue corpuscles lie, make their appearance. The serous canals have, however, very different forms in the various organs. They appear as distinct plexuses of subcylindrical canals in the dense organs composed of connective tissue, to which reference has above been made, the form of the networks being in accordance with the stratification of the organ; so that in the tendons and fibrous organs the meshes are considerably elongated in the direction of the fibres, whilst in the cornea they are expanded into layers between the lamellæ, and are in communication with one another by comparatively few branches, that perforate the lamellæ in an oblique direction. In soft interstitial and investing connective tissue, like the perimysium, the canals appear extraordinarily wide, the dilatations in particular being in close proximity with each other, and the solid tissue, in which the canals are imbedded, being much diminished in quantity. Lastly, in all soft organs lying immediately upon the surface, in the most superficial layers of the capsules of the joints, in the serous membranes, and in the mucous membrane of the intestine, the solid portions are reduced to thin septa, which very incompletely separate the closely approximated spaces lined with cells. All these varieties constitute gradations of one and the same type, the terminal members of which present, on the one hand, the form of a cylindrical tube, and on the other, that of a lacuna; neither of them, however, represent the typical form, and it is consequently most appropriate to employ the term canal, since it expresses nothing definite with regard to their form.

In opposition to the importance which I attribute to the silvered preparations, various objections have been adduced, with all of which I am acquainted, since I have myself formerly had to meet them; but from my numerous researches I draw the

conclusion that all the indistinct appearances obtained by those who oppose my method, proceed from injuries, accidental rents, and alteration of chemical composition; and I still believe that no method is more suitable than mine. All objections to it may be disposed of in the words of Schweigger-Seidel: "The regularity of the figures, the constancy with which the same forms recur in certain localities, and the presence of nuclei, which, however, are not always equally distinct, in their interior, furnish satisfactory proof that they are not accidental formations." Schweigger-Seidel makes the above statement only in regard to the lines showing the presence of an

Fig. 78.

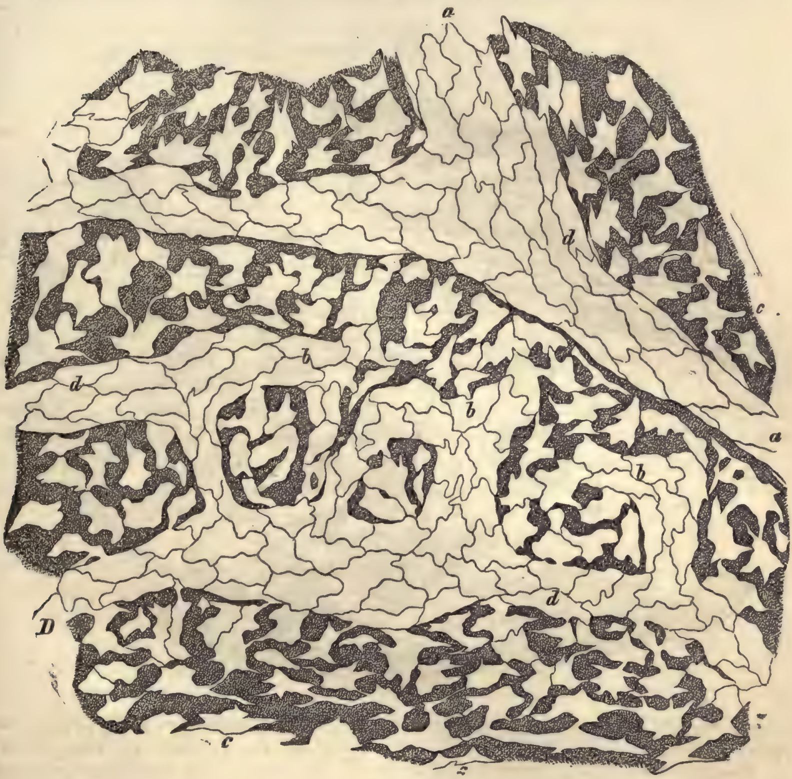

Fig. 78. Central tendon of the diaphragm of a Rabbit treated with silver. *a*, lymphatic capillaries with epithelium; *b*, commencement of the same; *c*, serous canals; *d*, transition of serous canals into lymphatic vessels most abundant at the border D. Magnified 300 diameters.

epithelium, and maintains that the indications of the presence of serous canals, after the removal of the epithelium, originate in an albuminous layer, subjacent to the epithelium, and consequently upon the surface, and not in the interior of the connective-tissue lamina. I do not, however, quite comprehend why Schweigger-Seidel leaves quite out of consideration the markings produced by silver in the cornea; for in the cornea it is quite easy to demonstrate that the layer on which the silver acts is not equivalent to the anterior surface of the cornea, which first comes into contact with the solution of silver, but not unfrequently rather lies in close approximation to the membrane of Descemet. From the consideration of this one point, the doubt which he has expressed could be overthrown, and the proposition above advanced be also maintained in regard to the silvered markings of connective tissue.

The serous canals represent spaces which are continuous with the lymphatic vessels, and it may even be said that they constitute the roots, so frequently sought after, of the lymphatics. As a proof of this, the following facts may be added: 1. In silvered preparations, a direct transition of the colorless passages of the serous canals into the smaller lymphatics may be observed. Successful preparations of the central tendon of the diaphragm show in the most distinct manner the transition of the small cylindrical serous canals (see fig. 78) into the lymphatic capillaries. The latter, at their very commencement, frequently present dentated contours, and at the

Fig. 79.

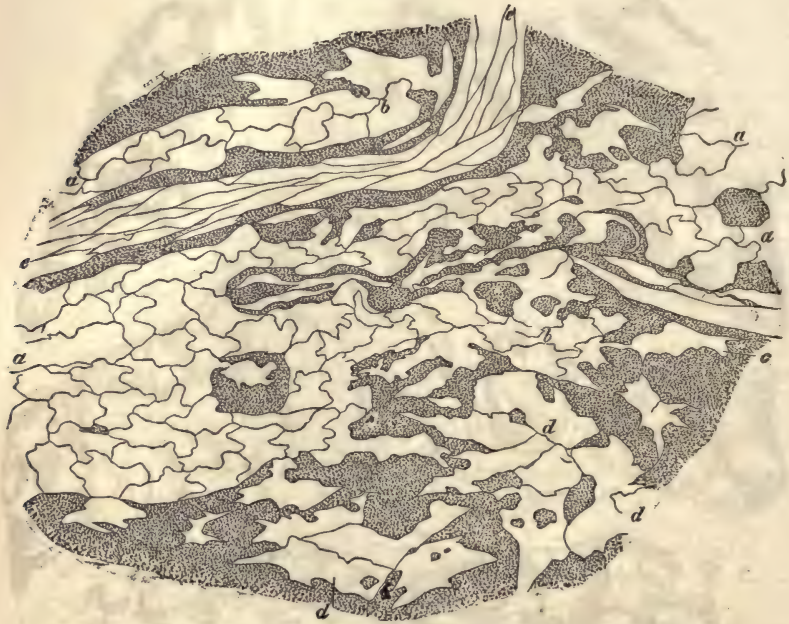

Fig. 79. Central tendon of the Rabbit, treated with solution of nitrate of silver, the most superficial serous layer immediately adjoining the pericardium being shown. *a*, lymphatic capillaries; *b*, their origin; *c*, serous canals with communications; *d*, serous canals equal in width to the origin of the lymphatic vessels; *e*, blood-vessel with epithelial cells. Magnified 300 diameters.

bottom of these depressions the limits of the lymphatic vessels very frequently become insensibly lost in the serous canal system. This disappearance of the boundaries of the lymph vessels it is very easy to understand is so much the more obvious in proportion as the canal system is wider, and is consequently particularly well marked in the serous membranes and other analogous structures (fig. 79).

In preparations of this kind it is important to avoid everything that may produce alterations in the structures under examination; for if the contours of the lymphatic vessels and serous canals are in the smallest degree rendered indistinct and hazy, it is impossible to determine accurately the nature of their connection. But such blurred images are always obtained if the epithelium has not been carefully removed previous to the impregnation of the preparation with the solution of silver. His ap-

pears to have had only such indistinct specimens before him, as he believed that an unskilled observer might remain in doubt as to the continuity of the contours.*

2. If the lymphatic vessels be injected towards their rootlets, it is very easy, even with an insoluble injection, to produce extravasation into the tissue, by which it becomes more or less stained. Under the microscope we may then see in the softer tissues only a dense mass of coloring matter, without any of the ordinary canals being visible; harder tissues must consequently be selected, if we desire in this way to ascertain the path followed by the injection. In the fascia of the thigh of the frog, forming the wall of a lymph sac, I have succeeded in filling canals containing connective tissue cells with granular coloring material, by injecting the sac; and we may also force very fine injections through the lymphatic vessels of the cutis into the subcutaneous connective tissue, the fluid passing directly into channels that precisely agree in their form with the plexuses containing healthy pigment, *i.e.*, the ramifications of the so-called pigment cells; indeed, the injection may sometimes be propelled into the plexus of pigment cells itself. We cannot, therefore, entertain any doubt that the injection, if it escape from the capillary lymphatics, enters into channel-like spaces of the tissue, which are nothing else than the serous canals themselves, since they here contain the pigmented connective tissue cells. Moreover, in all soft tissues, as, for instance, in the villi of the small intestine, plexuses first make their appearance; and then, when the injection has been driven with great force, the diffused tense infiltration is produced, in which no determinate figures are discoverable. Against these results it has been objected, and to a certain extent justly, that such appearances are due to over-distention, and originate in extravasation or rupture of the tissues; and it is certain that they do not appear with the above-named injections, unless very considerable pressure has been applied. In the mean while, the injection of the substance of the villi occurs even when only very slight pressure has been employed; and we here possess a very good means of control by a comparison of the results obtained with the natural injection that takes place with the chyle. The same appearances are presented in both instances, of a plexiform arrangement of chyle drops around the central lacteal in the first instance, and ultimately of chylous infiltration of the whole parenchyma of the villus. Can it be possible that such a plexiform appearance of the chyle masses has given rise to the belief that the lacteals in the villi form a dense network still closer and more compact than that of the blood-vessels?

The open communication existing between the serous canals and the capillary lymphatic vessels enables the latter to receive substances from the former; and the facts that have already been adduced, in regard to the behavior of the villi during chymification, afford sufficient evidence of the passage of a lymph current through the interstices of the tissues (serous canals) into the rootlets of the lymphatic vessels. Moreover, the passage of the cellular elements of the connective tissue from the serous canals into the lymphatics, although not as yet directly witnessed, is in the highest degree probable, since they migrate from place to place within the lumen of the former. Judging from silvered preparations, the communication between the rootlets of the lymphatic vessels and the serous canals is often so free as to render it difficult to determine the limits between them; this can, indeed, only be accomplished by determining the existence of an epithelium, and considering that the lymphatic vessels commence where the epithelium first makes its appearance.

* *Zeitschrift für wissenschaftliche Zoologie*, Band xiii., Heft 3, 1863.

The conclusions that have been here stated have by no means obtained general acceptance, and it must be acknowledged that further evidence is still required. We should endeavor to effect the physiological impregnation of the tissues with insoluble coloring or other particles, and subsequently to stain them with silver, in order to establish the fact that the absorbed material passes from the serous canals into the lymphatic capillaries; the evidence would be perfectly satisfactory, were it possible to propel the particles, whilst the preparation is under observation with the microscope, directly from the serous canals into the lymphatics. I, however, venture to hold that the theory as above stated affords an explanation of all the facts at present known, whilst others are not equally comprehensive. In order to render this evident, let us consider the facts on which the supporters of other views rely. Ludwig and Tomsa, for instance, regard the fissures they have discovered between the canaliculi of the testis as the origins of the lymphatic vessels, and they undoubtedly lie so close between the parenchyma,—not unfrequently investing the blood-vessels,—and the connective tissue is withal so small in quantity, that it is scarcely possible to look in this organ for other roots of the lymphatic vessels, that is, for a serous canal system. Ludwig and Zawarykin injected similar lacunæ in the kidneys surrounding the tubuli uriniferi. Tomsa made injections of the nose of the dog, and saw plexuses suddenly proceed from the injected capillaries, which he regarded as transverse sections of lacunæ intervening between the muscles, or fasciculi of connective tissue. At the same time, their fissure-like form was not demonstrated by him, and both his illustrations and descriptions agree equally well with my explanation, especially as it appears from them that fusiform cells (connective tissue corpuscles) are found at the borders of the injected canals. In the case of the kidneys, I have not been able to convince myself that the lacunæ in the tissue, serving as origins for the lymphatic vessels, are fissure-like in form. In regard to the lymph lacunæ of the testis, whether they exist to the extent described by Ludwig and Tomsa, or are less developed, they can afford no evidence on the mode of origin of lymphatics in other organs; for His and Tommasi have demonstrated that they are lined by the characteristic epithelium of the lymphatic capillaries, and hence are most probably analogous to these rather than to serous canals. The other theory, which refers the rootlets of the lymphatic system to the connective tissue corpuscles, rests on a fact which is also in full accordance with my view; namely, on the connection of the cells of the tissue with the dentated rootlets of the lymphatic vessels (Kölliker). I certainly do not participate in the doubts entertained by many respecting the lymphatic nature of these rootlets. It is true, indeed, that we cannot ordinarily perceive any current traversing them, since the fluid is as clear as water; but in one instance I was able, after protracted observation, to see a cell projecting from the terminal angular extremity of one of these rootlets gradually become absorbed into it; and which, in its brightness, its refractile power, and its size, completely corresponded with those tissue cells which are in contact with the lymphatic vessels; as it was entirely absorbed, it was immediately conducted, with moderate rapidity, but apparently passively, to one of the main trunks. I have not as yet been able to observe one of the stellate or fusiform connective tissue cells, which join with these lymphatic vessels, or lie quite on their exterior, to be pushed onward in a similar manner into the lumen of the vessel; yet I regard it as probable that this may sometimes occur. The above observation renders it more than probable that the tissue cells are not strongly adherent to the vascular wall, but lie in cavities which are continuous with the lumina of the lymphatic vessels. Large granular cells may also be seen in the interior of the larger-sized vessels of this description, lying near the wall, and at moderate distances from each other. These are considered by Kölliker to be collections of fat molecules constituting the remains of the primary formative cells; they usually present pale but well-defined outlines, possess numerous small teeth and projections on their surface, some of which enter the cavity of the vessel, whilst others penetrate the surrounding tissues. These cells do not give the impression that they are undergoing disintegration, but rather appear to me to be simply the connective tissue cells which hang from the interior of the larger vessels, and still remain attached to their walls. It might, indeed, be considered that these lymph passages or rootlets simply constitute expansions of the serous canals, leading to others by means of their closely proximated pointed processes, and an endeavor be thus made to prove that the serous canals and lymph passages are continuous. The question may be asked, do these persistent connective tissue cells under any circumstances develop into epithelial cells? I confess that I am unable to give a positive answer, and shall only here remark that, like Kölliker, I have been unable to obtain any evidence of the presence of an epithelial investment in these vessels by the action of nitrate of silver. After being injected with this fluid, the largest branches near the spine exhibited only confused lines which might be regarded as indications of an epi-

thelium, whilst in the smaller vessels branched cells became colored, around which were a number of fine lines resembling coiled fibres. Whether, as from this account appears probable, the peripherical portions of the lymph canals are destitute of an epithelium, or whether such an epithelium may yet be demonstrated by further investigations, all the peculiarities of these vessels agree in a most remarkable way with the view of the origin of the lymphatic vessels from serous canals. It is not difficult, from these considerations, to obtain additional evidence in favor of my theory; nevertheless I do not venture to do so, since we are treating of peculiar and, so to speak, embryonal tissues of lymph capillaries that are, perhaps, as yet destitute of epithelium, and in a very early stage of development; connections and communications may therefore exist at this period, which at a later stage are in some way or other modified or altogether abolished.

If now we may consider the system of serous canals as the origin of the lymphatic capillaries, the former system of tubes appears to be adapted for the conduction of the proper fluids of the tissues, whilst the latter constitutes the collecting tubes which carry off the superfluous fluid. Regarded from this point of view, the comparison of the structural character of the two systems is of great interest. Both are only sparingly present in the denser tissues that are permeated by only moderate quantities of nutritive fluid, as in the case of tendons; on the other hand, in tissues like the central tendon of the diaphragm and the mucous membrane of the intestine, in which the current of the nutritious fluid of the tissue is extraordinarily rapid, the lymphatic vessels are very abundant and wide in relation to the total sectional area of the serous canal; lastly, the serous canal system may have a great extension in relation to the entire efferent system of the lymph path, in which case the tissues are very soft and juicy, and the fluid in their interior undergoes only slow interchange, and is, perhaps, on this account, especially adapted to the formation of new cells. To the last category probably belong the looser masses of connective tissue which invest the several organs, and unite the interstitial connective tissue layers, on the one hand, with the serous and synovial membranes on the other. In point of fact, the outer layers of these tissues are very defective in continuity, whilst the serous canals are extraordinarily wide; the solid structures being only present in the form of thin membranes and trabeculæ, and we know from pathological processes how quickly a cellular infiltration occurs in them. In the tunica adventitia of the blood-vessels such cellular infiltrations have frequently been regarded as lymphatic vessels in a state of distention. In certain parts of the body this unusually wide serous canal system appears to coalesce, and form larger cavities, which then become invested with an epithelium: of this the serous cavities may be taken as an example in a physiological point of view, and the so-called serous cysts in a pathological. Where spaces of this kind form in or upon the tunica adventitia of the blood-vessels, we obtain sheath-like investments resembling the lymph sheaths of the tubuli seminiferi. To these belong the *perivascular* lymphatics described by His as existing partly in the membrane and partly in the substance of the brain and spinal cord; these are really interstitial spaces between the blood-vessels and the substance of the brain, continuous with a wide "epicerebral cavity" situated beneath the pia mater. That this last does not constitute a mere interstitial space may be maintained on the ground that it can be filled from the true lymphatic vessels of the pia mater. His has demonstrated the existence of an epithelium in the larger of these perivascular canals and sheaths, and they therefore represent the same grade of organization as the lymphatic capillaries. Macgillavry also found, in injected preparations of the liver, lymphatic sheaths around the blood-vessels, but it has not been satisfactorily ascertained whether they

are or are not lined with an epithelium. Stricker has, moreover, described a similar arrangement of sheaths around the blood capillaries of the lower eyelid of the frog; whilst Langer has shown that in this region only two lateral lymph tubes are present, which lie close to the blood-vessel, and occasionally unite by transverse anastomoses which cross the vessel like a bridge. It further appears from Langer's careful investigations in the frog, where the large blood-vessels are ensheathed by lymph sacs, or by processes of the lymph sacs, that from the point of their entrance into the different organs an "invagination of the blood-vessels by the lymphatic tubes is no longer to be distinguished;" in the serous and mucous membranes two lymph vessels, but in the interior of the parenchymatous structures only a single lymphatic vessel accompanies each artery. These investigations afford an important caution against too hastily admitting the existence of lymphatic sheaths around the blood-vessels. Many authors were formerly inclined to ascribe a perivascular system of canals to the blood-vessels of other organs, or at least to seek for lymphatic sheaths generally within the tunica adventitia of the blood-vessels. But this only is certain, that in the latter situation the serous canal system presents an extraordinary expansion, and is on this account predisposed to cellular infiltration.

The fluid contents of the serous canals, as well as of the lymphatic vessels, that is to say, the lymph itself, primarily comes from the blood; it is therefore a question of peculiar importance to determine what relation the serous canal system bears to the blood-vessels, and especially to the blood capillaries. At first sight it appears most natural to consider that the serous canals stand in the same communication with them as with the lymphatic capillaries. This was the relation which the authors of the last century understood by their vasa serosa, vessels which, on account of their small calibre, only permitted the passage of the colorless serum, and arrested that of the corpuscles. Leydig has translated this view into modern language, in stating that the connective tissue corpuscles are continuous not only with the lymphatic vessels but also with the blood-vessels. Führer, and before him Lessing, had already maintained the view that "the vasa serosa formed a plasmatic system connecting together the blood and lymphatic capillaries," in the interior of which the cells were situated. I formerly held it to be improbable that the serous canals were continuous with the blood-vessels, since I had not then given up the old view that the wall of the blood-vessels consists of a homogeneous substance. Since, however, it has been demonstrated by Aeby, Auerbach, and Eberth, by means of solutions of nitrate of silver, that the walls of the capillaries were composed of an epithelium, at all events in such organs as they had examined; since, moreover, the permeability of the vascular wall for the red blood corpuscles (Virchow, Stricker), and also for the colorless corpuscles (Cohnheim), has been noted under circumstances which, though certainly not normal, yet can nevertheless be so rapidly brought about that it is impossible to admit the occurrence of a qualitative change in the nature of the capillary wall, I consider it to be very possible that the serous canals may stand in the same open continuity with the blood-vessels as with the lymphatics. That such communications do actually exist under normal conditions is also rendered highly probable by the well-known fact that in the lymph, and especially in the chyle, not only colorless, but also red corpuscles may be discovered. Herbst instituted a series of experiments in which he augmented the total volume of the blood by slowly introducing blood, in the greater number of instances, but frequently also other fluids, as milk, into the jugular vein; and in these he constantly observed the

presence of red blood corpuscles in the abundant contents of the thoracic duct, and, where that fluid was employed, milk corpuscles also. Lastly, Dr. Rud. Böhm has very recently seen in silver preparations of the synovial membranes the serous canals become continuous with the blood capillaries in a manner very similar to that noted above as occurring in the lymphatic capillaries.

The Lymphatic Follicles.

In various parts of the digestive organs there are to be found, situated within the mucous and submucous tissues, and also in the spleen and the lymphatic glands, either projecting from their surface or appearing on section, small spherical bodies of the size of a millet seed—the so-called Follicles (see the article devoted to the digestive tract and the spleen). From the description given by Brücke, it was already known that the solitary follicles of the intestine and of Peyer's patches stood in intimate relation to the vessels of the lymphatic system. And this has been fully borne out by the more accurate modes of investigation recently adopted, but it has been further proved that the lymphatic follicles of the pharynx, tonsils, and lingual glands are also much richer in lymphatics than the remaining portions of the mucous membrane; that all these structures consist of tissues which recur in the lymphatic glands, and they may therefore truly be accounted a portion of the lymphatic apparatus. We must commence with the description of the follicles on this account also, that they represent a very simple type of the lymphatic gland.

The follicular tissue (adenoid substance of His, cytogenic tissue of Kölliker) is characterized, first, by its reticulum, and secondly, by the lymph corpuscle-like cells which are adherent to the reticulum.

The Reticulum, first demonstrated by Billroth, consists of very fine fibrils varying in their thickness, which for the most part pursue a straight course, and form a close network, the meshes of which are only sufficiently large to contain a few lymph corpuscles in each. The fibrils when fresh are extraordinarily pale, present a homogeneous appearance, and are distinguished from elastic fibres, to which, after the hardening of the gland, they present some similarity, by their lustre, and especially also by their chemical characters; acetic acid and soda making them swell up so strongly that they can no longer be perceived. The nodal points of this plexus are usually very small, and exhibit nuclei, but whether these are simply adherent to or contained within peculiar cells occupying the interior of the substance of the fibrils remains to be ascertained.

The lymph corpuscle-like cells, which constitute by far the greatest part of the follicular tissue, become isolated with extraordinary facility. They are contained in the milky fluid which flows when sections are made, and differ in some respects, and especially in their size, from one another (see lymph). The fibrils of the reticulum, situated at the periphery of the follicle, are in direct connection with the intercellular substance of the surrounding connective tissue; they attach themselves also to the blood-vessels, and especially to the capillaries, which traverse the follicle in the form of a wide-meshed plexus. The vessels are thus supported by a frame-work of fibrils, and hang freely in the spaces of the meshes.

The relations of the lymphatic vessels are of special interest. It has been a subject of dispute whether the follicles are rich or poor in lymphatics; the presence of lymphatic vessels in the follicles has even been altogether denied,

and the conclusion drawn that the follicles are of no special importance in the lymphatic system. It is true that lymphatic vessels are not present in the interior of each individual follicle; for even the most complete injection of the lymphatic vessels of the intestinal canal, as was pointed out by Teichmann, leaves the interior of the follicles free, whilst Frey's injections of the tonsils have shown that here also, however abundantly lymphatics are distributed through the whole organ, none are present in the individual follicles. These injections have, however, shown that the surface of each follicle is invested by an extraordinarily close network of lymphatic vessels, the several branches of which are widely separated from those of the neighboring follicles. The results of the investigations of His and Recklinghausen have further shown, and the same thing may be recognized in the illustrations accompanying Teichmann's work, that it is common for the follicles of the intestine to be surrounded by a lymph lacuna, and for the lymphatic plexuses to have become so close that the several tubes coalesce with one another to form a single spheroidal fissure. These lacunæ or lymph sinuses (according to His) in some instances surround nearly the whole surface of the follicle, leaving only that extremity or pole uncovered which is directed towards the surface of the mucous membrane; the follicle therefore hangs freely in the lymph path, or in what we may consider as an enormously dilated portion of it. That we are here dealing with lymphatic lacunæ, analogous to the lymph sacs of the Amphibia, and not with simple interstices or spaces between the tissues, is obvious from the action of solutions of silver, which bring into view a distinct epithelium immediately continuous with that lining the efferent or larger tubes of the lymphatics.

The follicles of the digestive tract must therefore undoubtedly be regarded as belonging to the lymphatic system; they probably form lymph cells in their interior, which pass into the lymph lacunæ, and then constitute ordinary lymph corpuscles. The relations of the epithelium investing the follicle on the surface directed towards the lymph lacuna, and the presence or absence of persistent openings for the passage of lymph corpuscles, are points that still remain to be elucidated.

Relations to the lymphatic system, of so intimate a nature as this, have, up to the present time, only been demonstrated in the above-mentioned follicles, whilst really nothing is known respecting the lymphatics of the well-known Malpighian corpuscles of the spleen, though they otherwise agree in structure with the follicles of the intestine; and we are equally ignorant of the lymphatics of the rest of the splenic tissue. The relations of the Thymus, again, which essentially consists of follicular tissue, to the lymphatic vessels, has also not hitherto been demonstrated.

Lastly, there are also found in certain organs composed of connective tissue, as the peritoneum and pleura of Mammals, and the mesentery and urinary bladder of the frog, such large accumulations of lymph corpuscle-like cells in the interior of very vascular regions, as to cause them to present the greatest similarity to the follicular tissues, though here, again, no intimate relation to the lymphatic vessels is capable of being demonstrated. It is noticeable, however, that, in regard to the chief division of the blood-vessels, these structures differ from those of the lymphatic follicles proper; for whilst in the latter the main trunks are distributed upon the surface, the artery occupies a central position in each follicle of the spleen, so that these appear to represent a dilatation of the tunica adventitia: on the other hand, veins are altogether absent in the interior of the splenic follicles. All these differences in the arrangements of the vascular system are, however, insufficient to justify us in attributing to these structures a function dif-

ferent from that of the lymphatic follicles of the digestive tract; they, too, probably constitute centres of development for the lymphatic cells which are carried away from the splenic follicles, not indeed by the agency of lymphatic vessels, but by other passages, as by the veins which form a very dense investing plexus around them (Basler), and by the analogous structures of the serous membranes consequent upon their communication with the above-described cavities.

THE LYMPH GLANDS, GLANDULÆ LYMPHATICÆ.

Up to a very recent period, the structure of the lymphatic glands was classed with those in which no efferent duct could be discovered. The lymphatic vessels were seen to penetrate the surface of the gland at numerous points, as the vasa afferentia, and to emerge from the hilus of the gland as vasa efferentia; but in the interior of these organs the lymph path, especially in its relation to the glandular structure, was in the highest degree obscure. His, in the first instance, and subsequently Frey and Teichmann, have furnished intelligible accounts of their structure; and although their descriptions certainly differ in some few points, it nevertheless appears to me that these differences are of a subordinate nature, and that we may now consider a perfectly clear description can be given of all the structural arrangements presented by these glands.

The lymphatic glands exhibit, not only in different species of animals, but also in one and the same individual, a varying structure which is undoubtedly difficult to define; the first examination of preparations of the lymphatic glands produces a very confused impression, as may best be understood if it be borne in mind that the variability which in general characterizes the lymphatic system manifests itself especially in the structure of these organs. The lymph paths in particular exhibit the greatest variations in form, sometimes being tubular and at others fissure-like or lacuniform, both constantly and for the most part very suddenly passing into each other.

In the larger and generally also in the smaller lymphatic glands, two substances are distinguishable (fig. 80), which may be designated the *cortical* (A), and *medullary* (B).

It is true that these names cannot be taken in a strict sense, since if the medullary substance be regarded as occupying a central position surrounded by the cortical substance, we not unfrequently find, on the contrary, considerable portions presenting themselves at the surface of the glands, and this elsewhere than at the bottom of the depression which represents the so-called hilus of the gland, and is occupied with connective tissue, the tissue of the hilus. In the subcutaneous lymphatic glands of the dog, for example, the medullary substance constantly appears at the surface, forming spots which may be easily recognized with the naked eye by their white color, and are frequently separated from the remaining portions of the gland by a yellowish pigmentary border. In these glands no true hilus is present. It cannot be maintained that a sharp distinction exists between the two substances, and we shall hereafter see that there is no essential difference of structure; but that the follicles of the cortex, which are usually regarded as characteristic of it, find their complete analogy in the medullary substance.

Nevertheless it is advantageous, in the first instance, to distinguish between the two substances, since in many animals the difference between them is even macroscopically very perceptible, as in the ox and horse, in both of which the medullary substance presents an intensely brown color. The

finer points of structure are best defined and most clearly visible in the ox, and it was therefore very fortunate that His chose the glands of this animal for his investigations. If sections be made from fresh glands, especially with high powers, we usually see only a homogeneous tissue, in which small

Fig. 80.

Fig. 80. Vertical section of a lymphatic gland from the Ox. A, cortical substance; B, medullary substance. *a*, capsule; *a'*, trabeculæ; *b*, follicles; *b'*, follicular cords (medullary cords); *c*, lymph path, designated in the follicles lymph sinus or investing sinus; the fine fibres traversing this are omitted. Preparation macerated in alcohol, and magnified 25 diameters.

lymph corpuscles, and indeed successive layers of cells, are arranged so closely that an intermediate substance is only apparent at the very thinnest parts of the sections. For the purpose of demonstrating the different structures, it is expedient in the first instance to harden the glands; and this can best be accomplished by maceration in alcohol, after which extremely fine sections must be washed, or still better, gently pencilled out. When this has been done, sections of the medullary substance are found to present a dotted character; these, however, are not complete perforations, but are distinguished from the denser tissue in consequence of their much greater transparency, and also by the circumstance that they contain the pigment, and this in the most marked manner in the ox; with still higher powers (see fig. 81), we see that they are traversed by fine fibres which are frequently arranged in a stellate manner, and often contain nuclei or cells to which granular masses of pigment cleave. These fibrils unite to form thicker vasciculi of connective tissue, *the trabeculæ*, which are not unfrequently flattened; they lie always in the centre of the above-mentioned spaces, and constitute the main trunk from the sides of which the fine fibrils of the reticulum are frequently given off nearly at right angles; the latter are then attached on the other side to the cords of the compact substance (*medullary cords* of Kölliker; *medullary tubes* of His; *lymph tubes* of Frey).

These medullary cords (fig. 81) have the same structure as the tissue of the lymphatic follicles (see above), consisting consequently of a reticulum of fibres enclosing lymph corpuscle-like cells, and may correctly be termed follicular structures, or *follicular cords.* The reticulum is distinguished from the fibrous tissue of the light spaces by the circumstance that the fibrils are individually finer, and the meshes of the plexus, especially in the peripheric layers, are much smaller.

Fig. 81.

Fig. 81. Section of the medullary substance of a lymphatic gland from the Ox. *a*, follicular cords; *b*, trabeculæ; *c*, lymph path. Magnified 120 diameters.

For their most remarkable peculiarity—namely, their want of transparency, as compared with the light spots—the follicular cords are indebted to the large number of these cells. It must be admitted, however, that this most obvious difference between the cords and the lighter spots is but slightly marked in fine sections of the recent or in thicker sections of the hardened gland substance, before they have been brushed and washed, since in the latter also the lighter spaces are fully occupied with lymph corpuscles. And, on the other hand, the differences may again disappear if the brush has been too freely used, since then the reticulum alone remains in the follicular cords. From this it follows that the lymph corpuscles are by some means firmly retained by the latter, whilst in the more transparent portions of the lymph path they lie loose and unattached. It may be asked, how are the corpuscles fixed in the reticulum of the follicular cords? It is probably effected by the great compactness of the reticulum and the smallness of its meshes which retain any lymph corpuscles that are traversing it either by a natural or artificial current, and it is also possible that the lymph cells adhere more loosely to the trabeculæ, since they only touch by a few points of their surface.

The mode of fixation of the lymph corpuscles is a matter of considerable importance. If, by plunging the point of an injection syringe into its tis-

sue, we propel various solutions through the substance of a lymphatic gland, or inject the organ through its afferent vessels, we shall find that we are able to clear the more transparent parts of corpuscles as effectually as by brushing, whilst the follicular cords preserve their cellular contents almost intact. Only a very small amount of pressure is required to accomplish this—no more, in fact, than that at which the lymph current ordinarily traverses the gland. It may be fairly maintained, therefore, that the natural lymph current is powerful enough to wash away the lymph corpuscles contained in the light spaces; and we may further draw the conclusion that each separate lymph corpuscle only temporarily occupies this tissue. In other words, these light spaces only constitute a path by which the corpuscles can be conducted away, whilst the reticulum of the follicular cords constitutes their proper domicile.

Injections of the lymph and blood vessels of the lymphatic glands furnish evidence, however, of still other and more important differences between the lighter spots and the follicular cords (see fig. 82). The distribution of the blood-vessels, properly speaking, only occurs in the latter; they alone contain capillary networks, whilst the lighter spaces contain only the larger blood-vessels, which, proceeding from the trabeculæ, traverse them in order to reach the follicular cords. On the other hand, injections, whether made by puncture of the gland substance or through the afferent ducts, prove to us that the light spaces represent the true paths pursued by the lymph. They, for the most part, fill with great facility, and the injecting fluid, if composed of thick solutions of gelatine and some coarsely granular coloring material, remains confined and limited to their interior. If, however, the fluid is more watery, and the coloring material very finely divided, it penetrates into the follicular tissue, in all instances clearly entering from the periphery. In cases where a very tense natural injection of the mesenteric glands has occurred with chyle, it is easy to demonstrate the presence of chyle granules in the peripheric portions of the follicular tissue; from whence it follows that the follicular cords are not completely excluded from the lymph path. Thus it appears that although the reticulum is very compact near their surface, it will still permit solid corpuscles to penetrate from the lymph path into the interior of the follicle, and therefore conversely it is probable that material particles—lymph cells, for example—may pass from them into the lymph path.

We are thus able to differentiate three separate parts in the tissue of the lymphatic glands: (1) the follicular tissue; (2) the trabeculæ; and (3) the lymph path. And we must now follow the form and arrangement of these into further detail. The trabeculæ are direct processes from the sheath of the lymphatic glands (see fig. 80), and, like this, consist of connective tissue, together with, in many animals,—as the horse, sheep, and ox,—a considerable quantity of smooth muscular fibre (O. Heyfelder). The processes which the sheaths give off towards the interior of the lymphatic glands are at first flat septa, which, near the centre, break up into cylindrical or subcylindrical cords, the trabeculæ, which ultimately become continuous with the connective tissue of the hilus. At the surface of the gland the trabeculæ are situated at a distance from one another, and usually, in conjunction with the external sheath, enclose alveolar-like spaces, in such a way that the latter are only uninvested on the part looking towards the hilus. As they divide into rounded cords, the trabeculæ come into much closer approximation; the spaces which they invest are consequently smaller than the alveoli, and at the same time are in much more free communication with each other. The follicular tissue, as a general rule, forms rounded

cord-like masses, connected with one another in a plexiform manner; these are not usually perfectly cylindrical, but present projections, and are sometimes even quite moniliform. Near the surface of the lymphatic glands the follicular cords give off particularly well-marked dilatations of perfectly globular form, constituting the granules that, both on the surface and also on section, are clearly perceptible to the naked eye, and are commonly described as follicles. The cortically situated follicles of the lymphatic glands are thus nothing but the club-shaped dilatations of the follicular cords of the medullary substance, and may be the more easily identified with the latter, since not unfrequently large globular follicles are to be found deeply situated in the medullary substance. The follicular framework is so intercalated in the meshes of the trabecular system, that the superficies of the follicular tissue never comes into immediate contact with the superficies of the trabeculæ, and the spaces which intervene between the two are the lymph paths. The form of the latter consequently agrees

Fig. 82.

Fig. 82. Section of the medullary substance of a lymphatic gland from the Ox. *a*, follicular cord; *b*, trabeculæ; *c*, path pursued by the lymph; *d*, blood-vessels. Magnified 300 diameters.

with the form of the two above-mentioned tissues, so that at the superficies of the alveolar trunks they present an approximation to the form of concave spherical shells (lymph sinuses, His; investing spaces, Frey); whilst in the interior of the gland they simply assume the form of the spaces left by the trabeculæ of the follicular network. It is easy to demonstrate, from injected preparations, that the vasa afferentia, which, as is well known, are distributed on the surface of the gland, directly open into these concave

areas, or lymph sinuses, and thus suddenly become converted from cylindrical tubes into lacuniform spaces. With injections of solutions of silver it is particularly easy to recognize the immediate transition from one to the other, on account of the facility with which the epithelium of the afferent lymphatic vessels can be followed on the outer wall of the lymph sinus. It is, however, unquestionably a matter of greater difficulty to establish the origin of the roots of the vasa efferentia from the internal lymph paths. This is not in any measure due to any difficulty of filling the vasa efferentia with injection in the direction of the current. On the con-

Fig. 83.

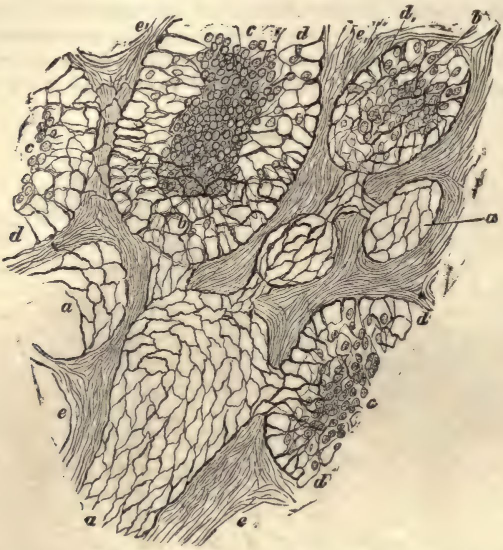

Fig. 83. Section from the medullary substance of a mesenteric gland of a Dog, after injection with silver. *a*, rootlets of the vas efferens, with a lining of epithelium in their interior. *b*, Dilatations of the channels, also lined by epithelium, and containing in their interior some gland substance with a follicular cord *c*; *d*, fibrils traversing the lymph path, upon which, again, as at *d'*, an epithelium may be distinguished; *e*, fibrous intervening substance, which at *e'* forms trabeculæ. Magnified 200 diameters.

trary, if the injection is sufficiently fluid, this may be accomplished with extraordinary facility, especially when the mode of injection by puncture is adopted. In such cases it will be found that the vessels of origin of the vasa efferentia have such a remarkably moniliform character, and communicate so frequently with one another, that they form quite a cavernous structure. The several canals in this cavernous plexus are so short that their union with the lymph paths of the medullary substance are far more difficult to recognize than if they were continuous with a few elongated canals. A general view of the relations existing in these parts may be best obtained from injections with solutions of silver (see fig. 83), and from these it can be established that the branches of the plexus, which up to this point have presented an approximatively circular section, suddenly undergo enormous dilatation, and into the lumen of these dilatations the several segments of the medullary substance imbedded in the hilus substance project, whilst the connective tissue walls of the cavernous plexus

become continuous with the trabeculæ of the medullary substance. The indications of an epithelium may be easily traced from the lymphatic tubes to the trabeculæ, and may further be followed on them through the medullary substance. But the trabeculæ and septa at the periphery of the glands exhibit also, in silvered preparations, the same characteristic indications of an epithelium; and I have so frequently been able to satisfy myself of the presence of this, that I may venture to say that they are invested by an epithelium throughout the whole gland. The characters of the lymph path at its entrance into and at its exit from the gland are essentially similar. The relations of the several parts may be most simply represented by considering a rete mirabile to be introduced between them, the several branches of which suddenly diverge from the extremity of the afferent vessel, and then proceed to divide and subdivide, becoming consequently more attenuated. These finer branches perforate the intervening layers of tissue in all directions, freely anastomosing with one another, and finally suddenly reunite in the extremity of the continuous and tubular efferent vessel. The follicular substance is chiefly developed in the dilatations near the point at which the vasa efferentia are attached, and from this point becomes gradually more and more attenuated, till it loses itself on the lymph path at the borders of the medullary substance.

This schematic representation of the arrangement of the lymph path corresponds to a fact of no small importance. Teichmann has shown that at certain points, in man especially, near the knee, retia mirabilia frequently occur in the place of true lymphatic glands, differing from the latter in the circumstance that the lumen of the several branches is clear and free from follicular tissue. Teichmann maintains that the lymphatic glands originate from these by accumulations of lymph corpuscles, which attach themselves to the interior of the vessels, and here form knots or clumps composed of follicular tissue.

This view of the mode of origin of the lymphatic glands, which is similar to that formerly proposed by Engel and others, agrees but little with the recent observations of Sertoli, who found that lymph canals lined with epithelium first made their appearance; around these the connective tissue increased; and in this, and consequently *external* to the original lymph path, accumulations of cells occurred to form the follicular glandular substance.

The structural arrangements here described as existing in the lymphatic glands can be most easily recognized in the glands of the ox and sheep. The glands of other mammals, and of man, present difficulties which are easily set aside if the fundamental structure of the lymphatic glands, as we now understand it, proves to be correct. In the lymphatic glands of oxen, the lymph path and follicular tissue may be distinguished with precision,(1) because the fibrous framework of the lymph path is beset with pigment both in the medullary and the cortical substance, whilst the follicular tissue is colorless; (2) because the follicular tissue through the entire medullary substance forms continuous uninterrupted cords, which for the most part exceed the lymph paths in breadth. In the lymphatic glands of man and the dog the relations of the medullary tissue are somewhat different, the lymph path here occupying relatively a much greater space than the follicular substance. Moreover, the trabecular system is much less completely developed, and it is not every section of the lymph path which, as in the lymph glands of the ox, is traversed throughout its whole length by a trabecula; for sometimes the position of the trabecula is not distinguishable, so that between two neighboring follicular cords there appears only a homogeneous framework of fibrils; whilst sometimes closer plexuses are formed by these fibres, which present nodal points analogous to the trabeculæ. Lastly, the follicular cords, especially in the lymphatic glands of man, present less sharply defined surfaces towards the lymph path than in the ox, the reticulum is of looser structure, and the lymph corpuscles adhere less firmly; and thus, by the too firm use of the brush, appearances ~~are easily~~ obtained, of which it is much more difficult to give a satisfactory explanation than in preparations

obtained from the ox. Lastly, it is to be remarked that the proper lymph tubes penetrate far deeper into the medullary substance. The lymphatic glands of man and the dog, again, differ essentially *inter se* in this point, that in man a highly developed hilus substance is present, giving a correspondingly distinct reniform shape to the glands, and only absent or sparingly developed in those of the mesentery, whilst it is usually altogether absent in the lymphatic glands of the dog, whilst the medullary substance and the efferent vessels, as already mentioned, are much more visible upon the surface. The lymphatic glands of the pig exhibit peculiarities of quite an opposite character; here the follicular structure preponderates in extent over the lymph path, and nodal dilatations appear throughout the entire medullary substance on the follicular cords; that is to say, true follicles are formed, which make their appearance on section when examined with the naked eye, and the lymph path is so narrow that its injection can only here be effected with the greatest difficulty. According to Franz Schmidt, in other parts of the body of the pig, as in the pharynx, exceedingly strongly developed follicles are found; but it requires still further investigation to determine whether this is a consequence of the fattening of these animals, as Schmidt thinks, or whether it results from some peculiarity of this genus.

A more exact investigation is still required in order to determine the relations of the epithelia to the several tissues of the lymphatic glands. I have been unable to discover any epithelial layer on the follicular cords. The mode of connection of the fibrous framework with the epithelium is of special interest. I have frequently distinctly seen that epithelial cells are continued from the surface of the trabeculæ upon the thicker fibrils (see fig. 83, *d*); these consequently possess an epithelial investment of the same kind as the nerves which traverse the lymph sacs of the frog. It still remains to be ascertained whether this relation is generally present or is only partial, and whether the follicular cords, as has hitherto appeared to me, are destitute of epithelial cells, and thus lie naked in the lymph path.

The Chyle, or milk-white fluid formed during digestion, and contained in the lymphatics of the intestine, and the Lymph, which is the colorless, slightly opalescent fluid contained in the remaining portions of the lymphatic system, coagulate like the blood, and then separate into an albuminous serum, and a clot, which last contains the morphological elements—the lymph corpuscles or cells. In addition to these there are found, though in very variable proportion, small granules of rather high refractive index, which were formerly termed elementary granules, and are in all probability minute drops of oil. In the chyle there are also extremely small points likewise consisting of oil, and termed the molecular base of the chyle; these are present in such enormous numbers as to impart to the chyle its opacity and dense white appearance; lastly, there are red blood corpuscles. The lymph corpuscles are now universally admitted to be identical in all their characters with the colorless corpuscles of the blood. They show in particular the same constantly varying form and the same phenomena of contractility, as long as they are living; whilst they assume the spheroidal form, which was formerly considered to be their natural shape, as soon as they die. The manipulations that up to a recent period were adopted for microscopical examination very easily kill them, and thus a fatal effect is produced by evaporation, by the addition of water, or of saline solutions containing more than 2 per cent. of salt. Even mechanical agencies, as the weight of the covering glass, are sufficient to rapidly extinguish all indications of life. Whilst the substance of the lymph cells during life is highly refractile, and even possesses a peculiar brilliancy, it becomes paler and dull after death; coincidently there appear small points (perhaps fat drops) in its interior, and in their centre a nucleus which is usually strongly granular. The corpuscles of the lymph, like the colorless corpuscles of the blood, are not all exactly alike; thus there are some which present a granular character, whilst others present the form of very large cells with multiple nuclei, and others, again, are very small, and were formerly not recognized as true cells, but were described as free nuclei. Undoubtedly in the latter by far the greatest part of

the body is occupied by the nucleus, so that this is often only invested by an extremely thin layer of extraordinarily pale cell substance, which very easily undergoes disintegration. Lastly, we also sometimes find in Mammals and Amphibia large lymph corpuscles with brown granules in their interior, thus constituting pigment cells. In the various sections of the lymphatic vascular system the quantity of these elements varies, and they especially differ in their number according to whether the organs from which the lymph vessels proceed are in a state of rest or activity.

From whence now do these various morphological elements flow? Where is their place of origin? Formerly it was believed that they only originated in the lymph path, and the elementary granules were regarded as representing the very commencement of organization; and even within a very recent period it has been sought to establish the view that the lymph follicles and the lymphatic glands are the only seats of origin of the lymph corpuscles, and that these continue to increase by fission after their entrance into the lymph path; but such processes of division have not been observed in any trustworthy manner, and I have only once had an opportunity of directly observing under the microscope how out of a lymph cell a young lymph corpuscle situated near the nucleus was suddenly ejected; I was not, however, able to ascertain how it originated. The formation of lymph cells in the follicles of the lymphatic glands, on the other hand, can at least indirectly be demonstrated; for the lymph which is carried by the vasa efferentia from the glands is always far richer in cells than that which is flowing towards them, and moreover the lymphatic vessels which come from the intestinal follicles, and especially from the Peyer's patches, furnish a lymph containing a far greater number of cells than the rest of the lacteals (Kölliker). The follicular substance of the lymphatic glands is probably to be regarded as the chief formative centre for the lymph cells; it would, however, be going too far to say that the lymph corpuscles proceed exclusively from the lymphatic glands. The very precise observations of Herbst and Teichmann show that cells are already contained in the lymph of man and mammals before it has traversed the lymphatic glands. In all probability such corpuscles proceed from the connective tissue in which the lymphatic capillaries are distributed, and in the form of contractile connective tissue corpuscles may easily have migrated from the serous canals into these capillaries. It is impossible to ascribe the office of the formation of lymph corpuscles exclusively to the follicular apparatus, or even to the lymphatic glands, because, so far as we at present know, true lymphatic glands are absent in the Amphibia, notwithstanding the abundance of cells in their lymph.

According to this, the question of the arrival of the lymph corpuscles in the peripheric plexuses of the lymphatics is connected with the question of the origin of the migrating connective tissue cells. In obtaining a reply to these inquiries, the researches very recently made by Cohnheim, and subsequently by F. A. Hoffmann, under my direction, in regard to the genesis of the pus corpuscles, are of great importance, since the characters of the latter agree in all respects with the lymph corpuscles, migrating connective tissue corpuscles, and colorless blood corpuscles. Insoluble coloring matters are, it is well known, rapidly absorbed by all these contractile cells when brought into contact with them. If, now, some such coloring matter, capable of being easily recognized (for which purpose vermilion is best adapted), be introduced into the bloodvessels of a living animal, the colorless corpuscles take up the particles into their interior; if, at the same time, an inflammatory process be excited in some organ, as in the cornea, pus

corpuscles containing this coloring matter may be met with in the inflamed connective tissue, and even in the healthy cornea, but it is especially in the loose interstitial connective tissue that some migrating corpuscles containing the pigment may be discovered. We can only draw the conclusion from this, that such corpuscles must have been sufficiently approximated to the circulating blood to be able to withdraw the pigment from the blood. The simplest view is that they have entered in the blood itself, and thus, previous to their migration into the tissues, were colorless blood corpuscles. On this ground Cohnheim is opposed to the theory of Virchow, according to which the pus corpuscles originate in the connective tissue itself, and maintains that pus corpuscles are nothing but vagrant colorless corpuscles, and consequently are formed in those organs to which we refer the origin of the latter; that is to say, in the spleen and lymphatic glands. The immediate consequence of this doctrine is that the healthy migrating connective tissue corpuscles, as well as the lymph corpuscles of the peripheric lymphatics, must be brought to the tissues with the blood, and that both originate in the spleen and lymphatic glands; the latter, however, in the circuit of the blood through them, would certainly furnish similar cells to those which are brought to them in the vasa afferentia, which would also pass out by the vasa efferentia. There are still some additional grounds of support to be adduced for this doctrine of the migration of the colorless blood corpuscles. Cohnheim in particular rests upon direct observation of the first stages of inflammation in the exposed mesentery of the frog, where he saw the colorless corpuscles, which, as usual whenever the blood current is retarded, accumulate in the lateral quiescent layer, and traverse the vascular walls, especially those of the veins, in order to migrate in the well-known mode; and thus the observation formerly made by Waller * in 1846, but again forgotten, except in England, under the predominant influence of Virchow's teaching, has reassumed its proper position. Hering has moreover observed in the mesentery, when spread out under the microscope, that the escaped colorless blood corpuscles enter into the lymphatic vessels ensheathing the bloodvessels, in order to be transported to other parts as lymph corpuscles. On these grounds we shall certainly be inclined to regard this doctrine as well founded; nevertheless, in spite of considerable attention to this question, I have been unable to arrive at any very positive conclusion, and cannot avoid making a few observations. In the first place, it is certainly not easy to follow a particular corpuscle through its whole course from the blood current through the venous wall into the surrounding tissue, or to exclude the suspicion that the escaped cells proceed, not from the vascular wall, but from the adjoining connective tissue layers; secondly, the migration does not occur immediately after the exposure of the mesentery, but only after the lapse of some hours, when the most serious retardations and disturbances of the circulation have occurred. It is true I have been able to observe the migration of colorless blood corpuscles under much more favorable circumstances, and without remarkable alterations of the blood current, in the tail of narcotized tadpoles, not only in the capillaries, but in the small veins and arteries, and on these grounds I should not object to accept the doctrine that the migrating cells of the connective tissue proceed from the blood current, were it not that (1) in consequence of the narcotization, a certain retardation of the circulation was present; (2) that it was embryonal tissue that was under examination; and (3) that other observations are adducible, admonishing us that, with such movable elements, and structures so disposed

* S. Kosinski, *Wiener Med. Wochenschrift*, 1868, Nos. 56 and 57.

to wander, we must exercise extreme caution. I have especially observed that not only colorless cells escape from the blood path, but that migrating corpuscles of the connective tissue penetrate into its interior. After their entrance they creep along with long processes applied to the wall, in order again to escape at another point. What should we say if, in the above observations upon the mesentery, the escaping cells prove to be only such penetrating cells, which have entered either at a neighboring point of the vascular wall (either of a vein or a capillary), or perhaps have crept on to a more distant point in the arteries, or have originally been formed in the surrounding tissue?

Whether the lymph corpuscles and the migrating connective tissue cells originate in the place where they are met with, and become converted into immovable connective tissue corpuscles, as I have already stated is not impossible, or whether they are brought to the tissues from some distant point in the blood current, the above experiments so far afford evidence that they must move in spaces which stand in direct communication with the interior of the bloodvessels. The larger the quantity of vermilion that is introduced into the blood current, so much the more abundant are the corpuscles containing pigment discoverable in the lymph sacs of the frog. Hering found that in narcotization with opium lasting for some hours, the lymph vessels of the liver became extraordinarily rich in lymph corpuscles, together with red corpuscles; and Toldt observed that if insoluble anilin was simultaneously introduced into the blood current, the lymph paths in the medullary substance of the lymphatic glands of the liver became tightly packed with blue-tinted cells (admittedly without the presence of free pigment granules), between which were heaps of red blood corpuscles. The red blood corpuscles constantly present in the lymph, and especially abundant in the chyle, were sometimes formerly regarded as being developed in the lymph path from lymph corpuscles, but more recently they have been considered to enter the lymph path by rupture of the vessels. According to still more recent experiments, however, showing the permeability of the walls of the bloodvessels (see the section on the bloodvessels), and the connection of the blood capillaries with the serous canals, the presence of red blood corpuscles is no longer remarkable. The serous exudations found in the larger cavities of the body exhibit in all their characters, in their capability of coagulation, as well as in the number and nature of their cellular elements, in their normal condition at least, the most complete coincidence with the lymph; it may, however, be remarked that it is not uncommon to meet in them with the large so-called granule spheres, which, when freshly examined, possess numerous contractile, constantly varying, extraordinarily fine fibrils or pseudopodia on their surface, and probably have swallowed the granules which are imbedded in their substance.

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CHAPTER X.

THE SPLEEN.

By WILHELM MÜLLER,

OF JENA.

The structure of the spleen is intimately associated with that of the lymphatic glands. In both organs numerous trabeculæ proceeding from the capsule divide and subdivide, containing in many animals muscular tissue, the contraction of which effects a shortening of certain vascular channels and the evacuation of the fluids contained in the parenchyma. In both organs the cytogenous or adenoid tissue is employed to invest at least a portion of the bloodvessels with sheaths containing numerous cells, the rounded appendices of which, rich in capillaries, constitute the follicles of the lymphatic glands and the so-called Malpighian corpuscles of the spleen. In both organs the wall of certain vessels undergoes a peculiar modification, characterized by the breaking up of the tissue into a plexus of embryonal cells, the interstices of which are permeated by the fluids contained in their respective vessels; in the one case by lymph, in the other by blood. It is a consequence of this agreement in structure that certain causes of disease produce similar pathological effects in both organs, as is seen in typhus, leucæmia, and certain forms of glandular sarcoma (Hodgkin's disease).

The spleen is not present in all Vertebrata. In the Leptocardia and Myxinoids, for instance, it has not as yet been demonstrated. In the remaining Vertebrata, which possess the organ, it is constantly included between the laminæ of the peritoneum. Its position, however, is various; according to whether it is developed in the meso-gastrium, the mesentery proper, or the peritoneal investment of the pancreas. The structure, again, presents varieties in the different classes of the animal kingdom; in the Ophidia and in the Saurians, the constituent which in all other Vertebrata is chiefly developed, is here rudimentary, whilst that which in the latter is an accessory apparatus, agreeing with the cytogenous vascular sheaths of the lymphatic and lymphoid glands, attains in the former its greatest development. In consequence of this mode of development, the spleen of these animals forms the link connecting the lymphatic and lymphoid glands to the spleen of other vertebrates. These peculiarities of structure justify us in proceeding to describe the spleen of Ophidia and Saurians separately from the remaining vertebrates.

The Spleen of Reptiles.—In Ophidia the spleen appears to the naked eye as a granular mass, situated at the upper extremity of the pancreas; but in Mammals it lies on the left side of the stomach, and presents a more homogeneous structure. It possesses a capsule composed of fibrillar connective tissue and fine elastic fibres. The interstices of the fibrils of the connective tissue contain, especially in the middle layers of the capsule, numerous lymph corpuscle-like cells. The deeper layers exhibit, in prepa-

rations that have not been injected, regularly arranged bands of smooth muscular tissue. In injected preparations a rich plexus of veins comes into view at this part, to the walls of which most, if not all, of the smooth muscles must be attributed.

The interior of the organ is traversed by septa given off at tolerably regular intervals from the internal surface of the capsule. The structure of these processes agrees with that of the capsule, and they intercommunicate with one another in the interior of the organ. They form stellate expansions; their connective tissue becoming infiltrated with lymph corpuscles, which in this modified form occupies all the interspaces of the proper parenchyma of the organ. This last appears in the form of spheroidal masses (globi or follicles), the diameter of which, in the ordinary domestic animals, varies from 0·5 to 0·75 millimetre. The follicles themselves are composed of cells and a retiform intermediate substance.

The cells agree with the lymph corpuscles of the animals in question, consisting of a mass of protoplasm containing a nucleus, but destitute of a cell wall. Larger morphological elements are constantly found intermingled with them, containing two or three nuclei which may be regarded as the

Fig. 84.

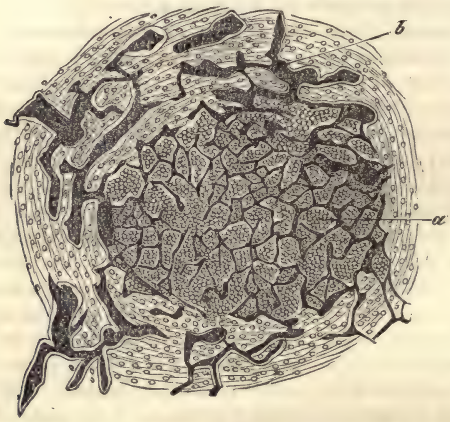

Fig. 84. From the spleen of the Tropidonotus natrix. *a*, follicle, with its capillary plexus ; *b*, septum, with venous plexus.

result of a process of multiplication. At the periphery of each follicle the cells lie more closely packed together than near the centre, and in the fresh state they are connected together by a pale, finely granular, tenacious intermediate substance. In preparations that have been hardened by diluted solutions of chromic acid, a plexus of delicate fibres may be recognized. This plexus is more distinctly fibrillar, and its meshes are more elongated near the periphery of the follicle than elsewhere, and the interspaces are here also filled with closely compressed lymph corpuscle-like cells. This more compact plexus extends beyond the limits of the follicles, so that neither in the fresh nor in the hardened state can a continuous investing membrane be demonstrated around them.

The blood-vessels of the spleen of Reptiles consist of arteries, capillaries, and veins. The artery enters the spleen of Ophidians at the part opposite the pancreas, which is sometimes hollowed out in the form of a hilus, and

runs towards the centre, enclosed in a membrane-like investment of connective tissue containing numerous lymph corpuscles. At this part it divides into fine branches, which run towards the centre of the several follicles, where the smallest arterioles break up into a very characteristic capillary plexus. This forms meshes of 0·015—0·03 millimetre in width, which contain the parenchyma. The meshes are polygonal in form, strongly resembling the capillary plexuses of the fœtus; the calibre of the vessels exhibits, within a short space, variations of considerable extent, and the wall, whilst it in part corresponds precisely to that of ordinary capillaries, is in part constituted of distinct nucleated cells, which are with difficulty, and only through their somewhat more elongated form, distinguishable from those of the adjacent parenchyma. Near the periphery of the follicles the meshes of the capillary plexus diminish, whilst the diameter of the vessels increases in size, and they at length become continuous with a very close plexus of thin-walled veins, which wind around the follicles. These veins, which in some parts consist only of a thin connective-tissue layer containing numerous cells, transmit their blood into larger branches, lined with epithelium, and provided with layers of muscular tissue, which partly run along the septa in the interior of the organ, and partly in the deeper layers of the capsule, to reach the point of entrance of the artery, by the side of which they emerge from the organ as the splenic veins. The fact that the walls of a portion of the capillaries in the spleen of Ophidians very frequently present features reminding the observer of their embryonic structure, naturally suggests that besides a continuous new formation of lymph corpuscles, a similar neoplastic formation of capillaries may also take place, but what relation this process bears to the function of the organ is not at present known. The plexus of thin-walled veins which wind around the periphery of the follicles resemble the lymph spaces that surround the periphery of the follicles of the lymphatic glands. They represent at the same time the rudiment of a splenic pulp. If we imagine the elements of the walls of these canals to become developed into a plexiform tissue traversing the lumen of the vessel, we shall obtain a tissue presenting the essential characteristics of the splenic pulp, as it occurs in other vertebrate animals. No observations have hitherto been made on the lymphatics or on the nerves of the spleen in Reptiles.

The Spleen of Fishes, Amphibia, Chelonians, Birds, and Mammals.—However various may be the structural arrangements of the spleen in these several divisions of the animal kingdom, the essential features of construction are the same in all. The organ is constantly invested by a capsule which sends off processes into the interior. These either hold some determinate relation to the venous system of the organ, forming venous sheaths, septa, and trabeculæ, or to the arterial system in the form of arterial sheaths. The interspaces of these tissues are filled with the peculiar parenchyma termed the splenic pulp.

The Capsule of the Spleen.—The thickness of the splenic capsule appears to bear a direct proportion to the whole volume of the organ. In the embryo it is invested by a short form of cylinder epithelium, resembling the ordinary epithelium of the peritoneum. As the organ grows this becomes flattened, and in adults forms delicate, partly square, partly rhomboidal plates. In all Vertebrata fibrillar connective tissue, with which elastic fibres are abundantly intermixed, enters into the composition of the capsule. In Fishes and Amphibia, so far as observation has at present extend-

ed, these elements form the entire capsule. In the higher Vertebrata, from the Chelonians upwards, a variable proportion of smooth muscular fibres, which are always situated in the deeper layers of the capsule, is likewise present. In Carnivora, in the Ruminants, and in the Pig, these are so largely developed, that the physiological experiment of merely dipping the spleen into warm water furnishes evidence of their presence, whilst in the Rodentia and Cheiroptera they are much less abundant. Muscular fibres, even if they are constantly present, are only sparingly distributed in the splenic capsule of Man.

Septa and Sheaths of the Veins.

The association of these two constituents is justified by the constancy of the relation which they bear to one another. From the deeper layers of the splenic capsule fibrous bands are given off at regular distances, which are recognizable with the naked eye, and become continuous with cylindrical cords, the so-called trabeculæ of the spleen that penetrate its substance. They communicate with one another by lateral branches, and form a network traversing the entire organ. Their structure is identical with that of the deeper layers of the capsule, except that they for the most part contain bands of smooth muscular fibres. A certain number of these trabeculæ extend constantly between the ramifications of the veins, and become attached to their walls either at acute or at right angles. The structure of the latter is thus rendered more complex, as the splenic veins have already at their point of entrance into the organ received an annular investment from the capsule which soon coalesces with the vascular walls. The latter thus acquire remarkable firmness, and from the increased strength afforded by the attachment of the numerous trabeculæ are prevented from collapsing, presenting in consequence, in this respect, a certain similarity to the sinuses of the dura mater. This modified venous wall sooner or later becomes incomplete, whilst the connective tissue layers containing muscular fibres split into small bands, between which the lumen of the vessel is only limited by the epithelium layer and by a delicate layer of connective tissue containing numerous cells, and representing the tunica intima. This assumption of a fibrous character by the external vascular layers may even commence in the trunks of the splenic vein, as occurs in the Ruminants; but more frequently, as in Man, it is first observable in the smaller branches. The slender bands containing muscular fibres, into which the sinus-like venous wall divides, run for a greater or less distance along the branches, ultimately becoming detached and uniting with the trabecular network of the organ (W. Müller). The object fulfilled by the connection of the trabecular network of the spleen with the walls of the veins is sufficiently obvious. The longitudinal bundles of muscles belonging to the latter tend to shorten the canals, whilst the trabeculæ which are laterally attached to them widen them, and thus conditions favoring the the discharge of fluid from them are established (Tomsa). A coincident contraction of the muscles of the capsule and of the trabeculæ must, moreover, exert pressure upon the intervening parenchyma which compels the movement of such of the constituents of the latter as are capable of changing their position to those parts where the tension is least (W. Müller).

Arterial Sheaths.—At their entrance into the hilus of the organ the arteries receive a sheath from the capsule with which the proper vascular wall is loosely connected. This sheath consists of fibrillar connective tissue with

numerous elastic fibres, and a moderate proportion of cell elements lying between the fasciculi, the latter appearing partly as rounded lymph corpuscle-like bodies, and partly as elliptical nuclei which only present small masses of protoplasm at their poles. The sheaths accompany the arterial branches, without essential modification in their structure, to the points at which the arteries and veins previously running together separate from one another, which usually occurs in the arterial branches, of from 0·3 to 0·2 millimetre in diameter. From this point onwards the arterial sheaths present a remarkable modification in their structure, which consists in the conversion of their connective tissue into a cytogenous tissue, whilst at the same time it becomes much looser in texture. The connective tissue bundles throughout the whole thickness of the sheath become coincidentally much looser; their fibrils become more delicate, and lymph corpuscle-like cells are abundantly found in their interstices. A cylindrical sheath, rich in cells, is thus formed, which accompanies the arterial branches either to their entrance into the blood passages of the pulp, as in Fishes, Amphibia and Chelonia, or to their passage into the capillaries, as in Birds and Mammals. In the first-named animals it is only seldom that any further development of these sheaths occurs; in Birds and Mammals, on the other hand, rounded or ellipsoidal sharply circumscribed bodies, varying from 0·3 to 1 millimetre in diameter, appear with great regularity, termed the Malpighian bodies of the spleen, which are easily recognizable with the naked eye, on account of their whitish color. They represent, as is now generally admitted, local hyperplasiæ of the cytogenous connective tissue of the arterial sheaths. Their disposition upon the arterial branches to which they belong varies to some extent, according to whether they are developed from the entire circumference of the arterial sheath, or from only a definite point of it; in the former case, surrounding the artery to which they belong like a ring; in the latter, being situated eccentrically, or being only laterally attached.

The parenchyma of the Malpighian bodies is formed of cells and a retiform intermediate substance; the cells agree in their characters with the lymph corpuscles of the several animals, and they are constantly found in various stages of development, some being smaller, with a single nucleus, and others larger, with several nuclei. Like those of the splenic pulp, they are capable of executing amœboid movements, and are usually more densely crowded at the periphery of the Malpighian bodies than at their centre. When treated with solution of carmine, *cæteris paribus*, they become more intensely tinted than those of the pulp, though it has not been hitherto determined whether the deeper hue is the consequence of the presence of a larger proportion of protoplasm capable of imbibing the color, or to a difference in the fluid by which the protoplasm is permeated.

Associated with the cells is a delicate intermediate substance, the periplast of Huxley. This forms a network around the several cells or groups of cells, and when examined in the recent state, consists of a pale, extremely finely granular, tenacious material, which presents the form of delicate fibrils in preparations hardened in chromic acid. At the periphery of the Malpighian bodies the network becomes closer, the individual fibrils present a greater similarity to ordinary connective tissue fibrils, and the meshes become more elongated and narrow, though without actually forming a continuous membrane, as was first correctly demonstrated by Henle.

Pulp.—The tissue of the splenic pulp is composed of cells and of an intercellular substance. The former resemble the lymph corpuscles of the animal, and constantly appear as small uni-nucleated and larger multi-nucleated

cells, furnishing evidence of the occurrence of continuous processes of new formation. These become less deeply tinted with carmine than those of the Malpighian bodies, which they, however, resemble in exhibiting amœboid movements (Cohnheim). There may be frequently found in the splenic pulp, especially in adult animals, large cells which either contain granular pigment presenting the characters of Hæmatoidin, or rounded bodies resembling colored blood corpuscles. We may presume that the greater number of these cells containing blood corpuscles are occasioned by the migration of colored blood corpuscles into the protoplasm of the adjoining pulp cells.

The cells of the pulp are connected with one another by means of an intercellular substance. This was first observed by Tigri, and was more minutely described by Billroth. When examined in the fresh state, this appears as a pale, feebly refracting, very finely granular, tenacious substance, forming a delicate network between the protoplasm of the several cells. In chromic acid preparations it assumes the character of a tissue composed of homogeneous intercommunicating fibres.

At the periphery of the Malpighian corpuscles it becomes continuous, without any sharply defined line of demarcation, with the intercellular sub-

Fig. 85.

Fig. 85. From the spleen of the Hedgehog. *a*, a Malpighian corpuscle, with its vascular apparatus; *b*, splenic pulp, with the intermediary blood passages; *c*, the rootlets of the veins.

stance of the cortical layer. Near the capsule of the spleen, and also near the terminations of the capillaries and the origins of the veins, the intermediate substance becomes more strongly refractile as regards light, and more distinctly fibrillar. It here becomes continuous on the one hand by numerous processes with the connective tissue of the capsule, and on the other hand with the tunica adventitia enveloping the capillaries and rootlets of the veins.

The cells and intercellular substance of the pulp are not so closely compressed as are those of the Malpighian bodies; on the contrary, they frequently leave rounded or lacuniform spaces between them, in which, in spleens recently removed from the animal after ligation of the vessels and exposure to the action of chromic acid at 0° Cent., colored blood corpuscles constantly occur.

Bloodvessels of the Spleen.—Several arterial and venous trunks

usually penetrate into the interior of the spleen at the hilus. Both sets of vessels, invested with their sheaths, run for some distance in proximity to each other, branching like a tree as they proceed. When they have diminished to a diameter varying from 0·3 to 0·2 millimetre, the arteries separate from the veins. Their mode of branching continues to be tree-like without the occurrence of anastomoses between the branches. In this course the arteries give branches to their investing sheaths which break up into a capillary network, presenting few and wide meshes. This capillary plexus is richer in the Malpighian corpuscles, the meshes being particularly small near the periphery. The calibre of these capillaries, as a rule, is moderately small, but frequently unequal, and the structure of the wall also exhibits varieties, sometimes presenting the characters of fully developed and sometimes of embryonic capillaries (Huxley, W. Müller). At the surface of the Malpighian corpuscles the capillaries either open into the intermediate blood passages or into the rootlets of the veins. No proper veins accompany the arterial sheaths from the point at which they become cytogenous.

The arteries, as is usual among the Mammalia, quickly divide into numerous capillaries, that run a long course, and are invested by a delicate tunica adventitia composed of connective tissue. Generally speaking they exhibit the structure of fully developed capillaries, but in some places they present for a considerable distance walls composed of separate cells rich in protoplasm, constituting the transitional vessels of Schweigger-Seidel. After a longer or shorter course the capillary wall becomes much attenuated and finely granular, the nuclei surrounded with a distinct mass of protoplasm, their continuity interrupted, and finally the homogeneous wall breaks up into small striæ, to which the cells are attached, and which are continuous with the cellular and fibrous plexus of the pulp. Through the spaces thus produced in the primary capillary wall the blood escapes into the cavities formed by the cellular and fibrous plexuses of the pulp, that is to say, into the intermediate blood passages. From the latter the blood is collected into the rootlets of the veins. These commence as cribriform, interrupted canals, the boundaries of which are essentially formed of lymph corpuscle-like cells and a delicate intercellular substance, constituting a plexus with numerous lacunæ. After a short or, as in man and rabbits, a somewhat longer course, the vein obtains a continuous internal investment, consisting of a layer of fusiform epithelial cells with spheroidal nuclei, which not unfrequently project into the lumen of the vessel, the superjacent connective tissue layer becoming at the same time condensed, causing the lymph corpuscle-like cells to crowd more closely together, and the fibrillar intercellular substance to become more distinct, whilst it pursues a transverse direction, and forms a tolerably close plexus (Henle). The smaller venous branches unite like the branches of trees to form larger trunks, investing which a tunica adventitia, consisting of longitudinal connective tissue fibrils with interspersed cellular elements, soon makes its appearance. The cylindrical muscular fasciculi belonging to the adjoining trabeculæ attach themselves longitudinally to these branches, and immediately become firmly adherent to their walls. As this occurs every now and then at different points, the gradually enlarging venous ramuscules obtain their already described compact walls, resembling those of the sinuses of the dura mater, and which they retain up to their point of exit from the organ.

The foregoing description of the arrangements of the circulating apparatus in the spleen rests (1) on the observation that, in recently hardened spleens still containing

blood, both in the embryo (Peremeschko) and in the adult (W. Müller), the tissue of the pulp is constantly traversed by blood corpuscles; (2) upon the observation that artificial injections of the spleen constantly fill the same spaces which naturally contain blood corpuscles (W. Müller); (3) on the observation that, after the injection of the very fine seeds of the lycopodium, their presence in the pulp may be constantly demonstrated with the aid of the tests exhibiting the reactions of starch (Tigri). In opposition to this view is a second, which, originally advanced by Billroth, Grobe, Sasse, and Gray, has recently been supported by Kölliker. According to this view, the spleen, like other organs of the body, possesses a completely closed vascular system of ordinary structure, the veins everywhere forming plexiform anastomoses between which the parenchyma, traversed by capillaries, is contained in the form of cords, constituting the intervascular tissue cords of Billroth, or the bulbs of Grobe and Sasse. I have already, in my work on the spleen, explained why I cannot adopt this view. Moreover, in a series of the injected spleens of rabbits, and in the spleen of a monkey which was placed at my disposal by C. Thiersch, and more recently in examinations made upon the amyloid spleen of man, I have been unable to discover any facts favorable to the view maintained by Billroth and Sasse. Kölliker adduces in its favor, besides the points already mentioned, (1) that the current of blood would experience too much obstruction were it to freely traverse the pulp; (2) that the fresh spleen constantly presents an acid reaction; (3) that since the appearance of my work, no one has expressed himself in favor of the views therein contained; (4) that this view would constitute a novelty. The first objection is opposed by comparison of the blood pressure in the arteria lienalis with the pressure of the lymph in the vas afferens of any group of lymphatic glands. The second is easily confuted by applying the best neutral litmus paper; the third is overthrown by the work of Peremeschko, who is the only author that has thoroughly entered into the consideration of the question.

Lymphatics of the Spleen.—It is highly probable that the spleens of all vertebrate animals possess lymphatic vessels. They are divided into a superficial and a deep set. The former run in the capsule, and constitute a close plexus, from which trunks arise that pass with the trabeculæ into the interior of the organs, in order to anastomose there with the deeper set (Tomsa). The latter, as usual, accompany and form open networks between the arteries and their sheaths, and extend to near their terminations. According to the observations of Tomsa, they penetrate the cytogenous sheaths of the vessels and their circumscribed enlargements, forming a plexus which, near the periphery of these structures, is only incompletely surrounded by the cavities of the adjoining pulp.

Nerves of the Spleen.—The nerves of the spleen also accompany the arteries in their course. They consist chiefly of Remak's fibres. They appear, in part at least, to terminate in peculiar organs that invest the capillary terminations of the vessels (W. Müller). These organs form ellipsoids, in the long axis of which a single capillary vessel runs. The substance of the ellipsoid consists of a pale, very finely granular substance in which oblong nuclei are imbedded (Schweigger-Seidel and W. Müller). These are highly developed in the spleens of Birds and carnivorous animals, but are only rudimentary in those of Rodents and of Man. In the interior of their granular mass fine fibres of Remak occur, the mode of termination of which has not as yet been actually determined. They require further investigation.

Development of the Spleen.—In all Vertebrata the spleen proceeds from a segment of the peritoneum. The situation of this segment differs in the several classes. In Ophidia it is the peritoneal investment of the upper extremity of the pancreas; in Fishes, Frogs, and Chelonia, it is the mesentery of the small or large intestine; in the Salamanders, Lizards,

Birds, and Mammals, it is a prolongation of the mesogastrium from which the organ is developed. Its first appearance occurs in the form of a homogeneous thickening of the peritoneum, caused by increase of the embryonic formative cells of which it is composed. This thickening occurs very early in Man; it is already demonstrable at the period when the first budding out of the pancreas has made its appearance. At this time bloodvessels may be followed to the seat of the rudiment of the spleen (W. Müller).* At this period there may be observed in chromic acid preparations a very delicate pale network intervening between the embryonic cells; but whether this proceeds from the outgrowth of a few cells, as Peremeschko maintains, or from the detachment of the peripheric protoplasm of numerous cells, I am not able to decide. The further development of the organ occurs tolerably rapidly, so that in the human fœtus of eight centimetres in length the various constituents are already differentiated. The cells lying beneath the peritoneal epithelium become elongated, and form fusiform nucleated bodies, and similar ones at an early period invest the larger vessels. From both small processes are given off, which grow towards one another, and represent the commencement of the trabecular system. Along the arterial branches, denser accumulations of small nucleated cells may already be discerned, which are conspicuous in tinted preparations by their deep color, and these form by far the chief constituent of the pulp. This consists of cells with from one to three nuclei and a delicate intercellular substance, forming plexuses, the interstices of which are constantly filled with blood corpuscles. According to Peremeschko, there are now developed larger protoplasmic corpuscles in the tissue of the pulp containing from two to six nuclei, that are capable of performing amœboid movements, and which, towards the end of embryonic life, atrophy. In the further course of development the several constituents increase in volume, and a part of the fusiform cells of the capsule and the vascular sheaths develop into smooth muscular tissue. The arterial sheaths, containing numerous cells, are clearly distinguishable from the pulp, and from the middle of embryonic life the Malpighian corpuscles are recognizable. The cavities of the pulp may, about this time, be artificially injected (Peremeschko). From the commencement of differentiation of the several constituents of the organs, as this author has pointed out, the cells of the pulp appear paler and more delicate than those of the arterial sheaths. To explain this it must be borne in mind that both of these morphological elements develop from different textural formations, the pulp developing from the walls of the rootlets of the veins, the arterial sheaths with their Malpighian bodies from the connective tissue investing the arteries. It is of importance to establish this difference, because it furnishes the key to a series of comparative anatomical and pathological observations. Up to the present time, no facts have been ascertained in regard to the development of the lymph passages, or of the nerves of the spleen.

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CHAPTER XI.

THE THYMUS GLAND.

By E. KLEIN.

In Man and Mammals, at an early period of their existence, a placentiform lobulated body, called the thymus gland, which in point of structure must be associated with the peripheric lymphatic glands, lies behind the upper part of the sternum, and partly occupies the Incisura jugularis at the lower part of the neck. It is invested by a capsule rather loosely connected with the organ by means of vessels and fasciculi of connective tissue, the thickness of which increases with the size of the organ. The number and size of the lobes vary to a considerable extent. In dogs, in the pig, and in the cat, there are usually only two closely connected lobes of unequal size, which present an acute edge externally and below, but are remarkably thick at their surfaces of contact. In the calf, on the other hand, the organ consists of two oval placentiform lobes not presenting acute edges, and of nearly equal size, united together by a short cylindrical intermediate portion. The thymus of the new-born infant exhibits two or three lobes; when there are three, these are so arranged that a central thicker lobe has sometimes a larger and sometimes a smaller lobule on each side. The several lobules of the thymus in man, as well as in the dog, the cat, and the pig, may possess small appendices; and the fissures by which the lobes are produced are sometimes deep, and sometimes less strongly marked. Each lobe is divided into several lobules by fissures uniting at various angles, and these again are subdivisible into the ultimate divisions termed acini, alveoli, granules, or more correctly, follicles.

The capsule exhibits the usual structure of membranous connective tissue; its elements are, wavy connective tissue fibres united into fasciculi of various sizes, which decussate in all directions, and thus form a tolerably resistant membrane; fine elastic fibrils, which are partly united in a plexiform manner, and partly form large arches running in an irregular manner between the fibres of the connective tissue; a few lustrous, broad, strongly refracting bands, characterized by their looped course and resistance to the action of acids; and, lastly, cellular elements. These either resemble colorless blood corpuscles, or are provided with processes like the so-called stellate cells, or they may appear as large, finely granular, irregularly shaped bodies, usually containing a single small, spheroidal, highly refracting nucleus. On the outer surface of the capsule, or that which is directed towards the thoracic cavity, a single layer of pavement epithelium, resembling in form and character that of the peritoneum, may easily be demonstrated. The cells of this layer are polyhedral, and slightly elongated or rhombic in form, containing a vesicular spheroidal or elliptical nucleus.

If a portion of the capsule, carefully detached from the recently removed thymus of a dog, be spread out upon the slide with the aid of some indifferent fluid, and examined with a high power, besides the tissues and structures above mentioned we may discern also the deeply situated delicate ramifica-

tions of the bloodvessels, together with the sparingly distributed trunks of medullated nerve fibres; and lastly, certain peculiar cavities. At the points where two or more strong fasciculi of connective tissue decussate we meet with such large usually elongated spaces, which have somewhat sinuous margins bounded by a single layer of fusiform disproportionately large cells; the tissue immediately external to these, and forming a kind of wall to the cavity, is but little condensed. It is clear that we have here to deal with the cavities belonging to the lymphatic system, respecting which it is difficult to state decisively whether they are simple lymph sacs, or wide thin-walled lymphatic vessels. It is worthy of remark, that the quantity of lymph corpuscles they contain is extremely small, and bears no proportion to the size of the space.

The tissue bounding the several follicles of the thymus, and dipping into the interior of the organ from the surface of the several lobules, consists of a network of connective tissue, which, as may be particularly well seen in the thymus of the dog, is usually composed of fine fibres, arranged in the form of delicate rhombic meshes. These are generally filled with more or less closely packed large cells; but near the free surface of the follicles, where they are not confluent with one another, the cells are smaller and more crowded, whilst the tissue becomes so condensed as to form a kind of capsule. The individual follicles are either entirely thus encapsuled and isolated, as frequently occurs in the calf, or several may be united at their centric portion, as in the dog and man. On the whole, their structural characters are comparable with those of the Peyer's patches of the small intestine.

The form of the several follicles is elongated, spheroidal, or polyhedral, and those situated near the surface are always larger than those more deeply seated; those of the dog and the calf are usually elliptical in form.

The finer structure of the follicles displays the same morphological elements, with the same relative disposition, as the ordinary lymph follicles. According to His,* fine capillary bloodvessels, proceeding from the vessels running in the septa, penetrate the follicles at numerous points of their surface, and, in consequence of these frequent anastomoses, form a very close-meshed plexus. Between the vessels, and attached to them, as well as to the connective tissue of the septa, an exceedingly compact, but very delicate network is extended, chiefly formed by the anastomosing branches of multipolar cells, in the interstices of which are numerous lymph cells; in addition a narrow-meshed network may be distinguished, resembling the above, except in the absence of cells, and in the greater breadth of the trabeculæ, especially at their nodal points. The narrow-meshed networks are the prolongations of the interalveolar or interfollicular lymphatic vessels. Lastly, there occurs a third kind of trabecular structure in the form of strong elongated fibres, which are stretched between adjoining vessels, or between these and the septa of connective tissue. These are not much branched, and are attached by means of conical longitudinally striated bases to the vessels.

The contents of the follicles, that is to say, of the trabecular structures, consist of cells, which, according to their size, may be arranged in three categories. Of these the first, and by far the most numerous, are ordinary lymph corpuscles; the second are larger coarsely granular spheroidal bodies, composed of protoplasm, and containing one or several nuclei; and the third are Hassall's concentric corpuscles, of which Ecker† recognizes two

* *Beiträge zur Kenntniss der zum Lymphsysteme gehörigen Drüsen.* Siebold and Kölliker's *Zeitschrift für wissenschaftliche Zoologie*, Band x., p. 333.

† *Blutgefässdrüsen* in R. Wagner's *Handwörterbuch*, Band i., p. 115.

forms, one simple and the other compound. The former are spheroidal vesicles, varying from 0·0075 to 0·009 millimetre in diameter, containing in the interior of their concentrically striated sheath sometimes only a homogeneous mass with fatty lustre, but sometimes a nucleus and granular material. These last are as much as 0·027 millimetre in diameter, and are composed of several simple vesicles that are collectively invested and united together by a concentrically striated membrane. Both species of the concentric bodies occur, according to Ecker, at every stage of development; yet with increasing abundance as the gland gradually advances to complete maturity.

VESSELS.—In the calf and in man the larger branches running in the follicular septa divide into numerous branches that everywhere surround the follicles.* The arteries give off capillaries that penetrate into their interior, and after communicating by transverse branches, run in a radial direction, and terminate in circular vessels. As a rule the latter do not quite reach the centre of the follicles, but become continuous with veins which accompany the arteries.

The distribution of the vessels in the thymus of the dog presents some difference from that which has just been described. Here the larger trunks situated in the septa give off branches that penetrate into the interior of the follicles, and then break up at the outer part into a capillary network, by which they are completely filled.† The very wide spaces charged with lymph cells, which immediately invest the follicles, are in communication, by means of finer vessels, with the central parts of the follicles. M. His regards these spaces as lymphatics; but, according to my observations, it must still remain doubtful whether they are lymphatic vessels or sinuses investing the follicles.

According to the older views,‡ the follicles are hollow vesicles invested externally by a structureless membrane, and internally by a layer of connective tissue, their cavities all communicating with a common central canal.

Jendrassik§ has demonstrated that the elementary parts of the thymus gland are solid lymph follicles, in the central part of which a cavity is formed by softening. I find that these cavities only occur in the follicles of the thymus in man and the calf, and not always even there. The central part of the follicle, which, both in man and the calf, consists of a network of cells with interspersed lymph corpuscles, after prolonged hardening, easily becomes detached during manipulation.

In regard to the physiological atrophy of the thymus, it consists, according to His, of a gradual breaking-down and infiltration of the glandular tissue with fat, which extends gradually from the septa and the surface of the follicles towards their interior; but even in the earliest period, when there can be no question of atrophy, small isolated groups of fat cells may be found in the investing sheaths of the follicles.

* Ecker, *loc. cit.*, and His, *loc. cit.*

† Kölliker, *Gewebelehre*, p. 485.

‡ J. Simon, *A Physiological Essay on the Thymus Gland.* London, 1845. 4to. Gerlach, *Gewebelehre.* Mainz. 8vo, Lieferung 2 and 3. Ecker, *loc. cit.*

§ *Anatomische Untersuchungen über den Bau der Thymusdrüse, Sitzungsberichte der k. Akad. zu Wien.* 1856, Juli-heft.

CHAPTER XII.

THE THYROID GLAND.

By E. VERSON.

The term thyroid gland is applied to an organ composed of a *framework* of connective tissue condensed externally to a more or less thick investing membrane, and traversing the interior of the organ in the form of strong trabeculæ; and, secondly, of *gland vesicles*, sustained by the framework, which, as their name implies, constitute structures similar to the acini of a gland, but completely closed and vesicular.

The vesicles of the thyroid gland are composed of a thin transparent hyaline membrane, lined by epithelium, the cells of which are arranged in a single layer, and in fresh, uninjured specimens appear longer than broad, and are provided with a spheroidal nucleus, which may itself include one or several nucleoli. In this condition, however, the epithelium of the vesiculæ is only encountered in quite young animals when examined with the microscope immediately after having been taken from the living animal. In a very short time, even under the eye of the observer, the free surface of the cell wall may be seen to project irregularly, and spheroidal tenacious and hyaline drops, which after some time coalesce in the centre of the vesicle, gradually develop from the bodies of the epithelial cells. Usually, however, delicate lines of demarcation may be recognized between them, giving a faceted appearance to the clump of escaped and coalesced cell contents. Before these drops become intimately fused with each other in the centre they frequently indicate the path they are about to pursue by pseudopodial processes which partly adhere to the cell wall. These contents, at a more advanced age, and under pathological conditions, are converted into colloid, though they originally represent only the product of a physiological process.

The several gland vesicles present great variation in size, and even in adults some may be found which are of much smaller diameter than the largest of those discoverable in the infant. It appears that in extra-uterine life the progressive increase of the several gland vesicles, if any, is usually very small. On the other hand, in a human embryo of the fifth or sixth month, I have found their diameter to be 0·0252—0·0336 millimetre, whilst their diameter in the newly born already amounts to 0·1—0·16 millimetre, and may in adults exceed 0·2 millimetre. The gland vesicles of the tortoise are particularly well adapted for investigation, since they measure from 0·14—0·27 millimetre. Mammals possess in general very small vesicles, which sometimes, by their further growth, so press upon one another that the space required for the capillaries is only obtained by an inflexion of their opposite walls. Such conditions I found to occur frequently in the dog, where the walls of the vesicles form projections internally, in which the epithelial cells are seated like the voussoirs of an arch.

It is deserving of notice that the larger vesicles occupy the centre of the several lobules, or, where these are not present, the centre of the entire gland, whilst at the periphery they appear much smaller and are compressed and flattened in form.

The epithelial cells, as already mentioned, are always somewhat higher than broad, and do not vary remarkably either with age or with the species of animal. Thus, for example, in an embryo of the fifth or the sixth month they were from 0·006—0·0095 millimetre long, and from 0·004—0·005 millimetre broad; in adults they attain the length of 0·01—0·16 millimetre; in the dog, from 0·008—0·0126 millimetre; in the calf, of about 0·0105; in the tortoise, from 0·0168 millimetre, etc.

The framework of the thyroid gland is a direct continuation of the external investing membrane, and, like this, consists of fasciculi of connective tissue, with numerous elastic fibres and connective tissue corpuscles, which for the most part appear fusiform or branched. The organ is partially traversed by stronger bands which, on the one hand, are connected with the investing sheath, and on the other, isolate large groups of gland vesicles. In this way the thyroid gland of man is divided into primary and secondary segments, the line of division between which is recognizable by light furrows. In other cases, however, these strong septa may fail, and the whole glandular organ represent a continuous mass.

The connective tissue lying between the several gland vesicles of the individual segments is very sparing in quantity, and sometimes even it is difficult to discover between the walls of contiguous vesicles a few fibres accompanying the capillaries. Near the investing membrane, and between the peripheral vesicles, it is more abundant. If the fresh vesicles of the tortoise be isolated by means of needles, we find them invested by a fine network of fibres, which frequently bear branched cells.

The Arteries are large branches of the thyroid artery, and penetrate into the interior of the gland, following the course of the fibrous septa, dividing the organ into segments or lobules. Their branches accompany the secondary septa, and these again break up into large capillaries having a diameter of 0·006—0·01 millimetre, that form a network around the several gland vesicles from which again the veins take their origin. These, externally to the fibrous sheath, are characterized by the width of their lumen and the proportionate thinness of their walls.

The lymphatics, according to Frey, commence with cæcal extremities between the gland vesicles, and unite to form meshes surrounding the lobules, finally emerging from the surface of the organ as vessels of considerable size. The *nerves* appear as thick trunks of dark-edged fibres which adhere firmly to the vessels.

In man the thyroid gland appears to be composed of a median and two lateral lobules united by means of connective tissue. Other mammals, as the dog, calf, horse, etc., possess a thyroid gland consisting of two separated lobules lying on either side of the trachea.

A single median lobe occurs in Amphibia and Birds, which descends into the thoracic cavity.

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CHAPTER XIII.

THE BLOOD.

By ALEXANDER ROLLETT.

The red blood of vertebrate animals consists in part of a solution of various substances—the blood plasma—and in part of very small corpuscular structures of peculiar form.

The corpuscles are so abundant and so equally distributed through the fluid medium, that their interspaces are of microscopic dimensions, and fresh blood consequently presents to the naked eye the appearance of a homogeneous red fluid. The individual corpuscles do not all agree with one another in their characters, and hence several different kinds may be distinguished amongst them.

In the first place, we may distinguish between the colored and colorless forms, the number of the former predominating in healthy blood.

The colored corpuscles are more uniform than the colorless, amongst which several subdivisions must be made.

The Blood Plasma.—The blood plasma, or Liquor Sanguinis, when examined in the fresh state and in microscopically thin layers, is destitute of color. If a drop of blood be removed for a short time from the living body of an animal, fibrin separates from it in a solid form. But in reference to the coagulation of the blood,* we shall here only discuss the microscopic phenomena presented by the fibrinous clot. The fibrin, when in small quantities, separates itself in the form of delicate fibres decussating at various angles, though when in large only very gradually, as often occurs in the blood of cold-blooded animals ; or if larger quantities of fibrin quickly separate, the whole drop of blood solidifies, without any alteration of the microscopic appearances being perceptible. In this case the change that has occurred only becomes evident on moving or breaking up the mass when it has undergone coagulation.

If, on the other hand, we leave a few drops of blood for a little while to themselves, which may be best effected by attaching them to the under side of a glass cover in a moist cell, we shall observe that the coagulum embracing the corpuscles retracts from the borders of the drop, and that a zone of clear serum is exuded, which gradually increases in breadth.

Here also striæ and bands of coagulated fibrin may be isolated by breaking up the coagulum and thorough elutriation with water.

The fibrinous coagulum appears doubly refractile under the polarizing microscope.

We shall hereafter revert to the behavior of the blood corpuscles in the fibrinous coagulum.

The Red Blood Corpuscles.—A knowledge of the general structure of

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* Compare Kühne, *Lehrbuch der Physiologischen Chemie.* Leipzig, 1866, pp. 162 to 174.

these bodies cannot here be discussed, but will be taken for granted in the course of the following observations.

After the blood corpuscles had once been seen by Swammerdam in the Frog in 1658, by Malpighi in the Hedgehog in 1661, and by Leeuwenhoek in Man in 1673, numerous observations were accumulated respecting them, perhaps even to a greater extent than upon any other * morphological element of the animal body. Up to the present time, however, no structural arrangements have been discovered in them with the microscope that can enable us to furnish an explanation of all or even of the greater number of the phenomena they display.

Compared with other morphological elements of the tissues, the red blood corpuscles appear so peculiar, and are so readily and permanently alterable by the action of numerous and often not obvious external influences, and present so many remarkable appearances, that statements based upon mere analogy can only be received with the most profound distrust.

The results that have been obtained by direct observation and inquiry will therefore here first be given, in order that we may not become confused with theories that have been inconsiderately advanced; the views of various histologists, founded on their own investigations, will, however, be subsequently noticed.

Form and Color.—Throughout the whole series of vertebrate animals two typical forms are presented by the red blood corpuscles. They form thin disks, the contour of which is either circular or elliptical. The circular disks occur in Man and Mammals, with the exception of the Camel and Auchenia. The two last-named genera have, like all Birds, Amphibia, and most Fishes, elliptical blood corpuscles.

Amongst the Fishes only a few Cyclostomata (Petromyzon, Ammocœtes) are known to possess circular disks.

A small drop of human blood, brought as quickly as possible under the microscope in the form of a thin layer, exhibits densely crowded colored corpuscles.

Their color depends upon hæmoglobin.† The individual corpuscles, however, do not appear red like pure hæmoglobin, or its concentrated solutions, but of a yellowish or green tint, perhaps on account of its small thickness, just as the same color may be obtained if thin layers of concentrated watery solutions, or thick layers of diluted solutions, of hæmoglobin are examined, and this whether it be oxyhæmoglobin or reduced hæmoglobin, or a definite mixture of both. The red color of the blood is only exhibited under the microscope when large numbers of blood corpuscles are examined superimposed on one another.

Where a number of the corpuscles thus lie upon one another, as may occur by chance in every small drop of blood, there may also be seen, as F. Hoppe,‡ Preyer,§ and Stricker ‖ have shown, the characteristic absorption bands of hæmoglobin, providing that a spectrum apparatus of appropriate construction is connected with the microscope. Stricker has also demonstrated in the microscopic spectrum the conversion of the oxyhæmoglobin

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* For the older literature, see Milne Edwards, *Leçons sur la Physiologie et l'Anatomie comparée.* Paris, 1857, T. i., p. 41.

† Compare Kühne, *Lehrbuch der Physiolog. Chemie.* Leipzig, 1866, p. 196

‡ Virchow's *Archiv*, Band xxiii., p. 446.

§ Max Schultze's *Archiv*, Band ii., p. 92.

‖ Pflüger's *Archiv*, 1868, p. 651.

bands into those of reduced hæmoglobin on alternate exposure to O and CO.

The circumstance of the red blood corpuscles being the carriers of the coloring matter of the blood, confers upon them their obviously great importance in the organism at large, on account of the part which the hæmoglobin plays in the exchange of the respiratory gases.

As regards the form of the blood corpuscles when examined microscopically in fresh blood, the greater number of the isolated corpuscles will be found to present perfectly circular contours, and to be of nearly equal size (fig. 86, *a*).

The description that must be given of this form may be best understood

Fig. 86.

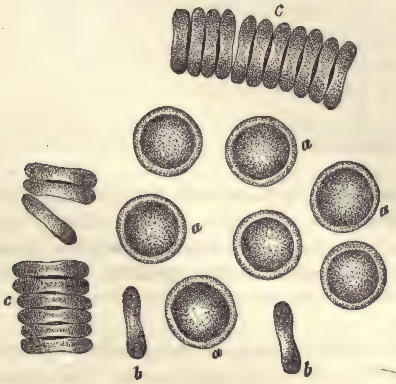


Fig. 86. Red blood corpuscles.

by making the corpuscles float by gentle taps on the covering glass. They then offer alternately the circular form and another completely different one, that, namely, of short rods with rounded poles and slightly hollowed surfaces, and resemble a finger biscuit, or a section carried through the axis of a bi-concave lens (fig. 86, *b*). Such a corpuscle, as it again revolves, places itself upon its edge again, and, in short, gives the impression of a rotating disk, with a thinner central portion, caused by a fossa-like indentation of the surfaces and a thickened border. A solid model of the blood corpuscle may be represented by the revolution of the curve *c c c* (Fig. 87) around the axis *a b*.

This form of blood corpuscle has also been termed the saucer-shaped. If the observer has convinced himself of the varying form of one and the same blood corpuscle, he will understand how in every blood drop there are presented to his eye numbers of such corpuscles standing on their edge. Nevertheless, the number of those which are lying on their flat surfaces is always much greater.

Lateral views of the blood corpuscles are also very commonly obtained on account of the adherence of the corpuscles in groups to one another by their broad surfaces. Chain-like forms are thus produced, which, when viewed laterally, resemble rouleaux of coin (fig. 86, *c*). The cause of this formation of rouleaux, which is frequent in fresh blood, has not as yet been discovered. It does not occur within the vessels. It is seen not only in

freshly drawn blood, but also in blood which has been immediately whipped, and thus freed from fibrin, though it may afterwards have remained for some time at rest.*

Besides the corpuscles just described, which are by far the most abundant, M. Schultze† constantly found in the blood of himself and of a few other persons a small number, varying with the period of the day, of minute bodies, differing from the ordinary corpuscles in their spheroidal form and

Fig. 87.

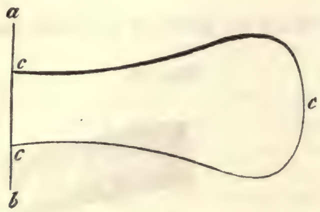
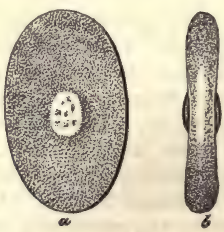


Fig. 87. Diagrammatic section of one-half of a blood corpuscle.

in some other peculiarities, together with transitional forms between them and the ordinary corpuscles. Further, in accordance with the frequently cited observation, though standing much in need of confirmation, of Lehmann,‡ the blood of the hepatic vein contains corpuscles of smaller size and more spheroidol form than usual, whilst those of the portal vein are of the ordinary kind.

The surface of the common form of corpuscle appears smooth, and the substance of the disk exhibits in its interior no indication of any difference in the index of refraction of its several parts. In passing from the centre

Fig. 88.



to the circumference, however, there is a distinct change in the color and transparency. In that position of the corpuscle in which the disk appears broadest and its edge most sharply defined, the centre is transparent, and the lateral portions are darker, whilst the extreme edge again presents a clearer ring. The latter is occasioned by the refraction which transmitted light experiences in the focal plane of the microscope when it traverses objects bounded by circular contours.§

* See Rollett, *Wiener Akadem. Berichte*, Band i., Abth. ii., p. 183.

† *Archiv für Mikroskop. Antomie*, Band i., p. 35.

‡ *Physiologische Chemie*, Band ii., pp. 85 and 232.

§ Nägeli and Schwendener, *Das Mikroskop*, Theil i., p. 184, *et. seq.* Harting, *Das Mikroskop*. Braunschweig, 1866, Band ii., p. 26, *et. seq.*

The appearance presented by human blood corpuscles is different from that of the corpuscles of animals with elliptical corpuscles. External to the elliptical border of the flat surface of the disk there may be observed, at least in Birds, Amphibia, and Fishes, a different structure when the disk stands on its edge. The optical section of the long axis appears here also slender, elongated, and rounded at the extremities. The long sides, however, have a projection at their centre (fig. 88, *b*). This prominence corresponds with an area situated near the centre of the disk, which, in comparison with the remaining colored mass of the corpuscle, appears whiter than the rest. This is sometimes more or less circular as in the Bird, or elliptical as in the Frog, Triton, and land Salamander; it is often quite smooth, but also frequently presents fine indications of dark points or striæ.

This spot corresponds to a structure which possesses no analogue in the fully developed blood corpuscles of Man and Mammals, but behaves itself quite differently from the remaining substance of the corpuscle, and shows at least as great an amount of agreement with the structure termed the nucleus in other animal cells, as do the nuclei of the different cells with one another. In common with most histologists, we shall designate this structure as the nucleus of the blood corpuscles.

The fully developed elliptical corpuscles of the Camel * and Auchenia are as destitute of a nucleus as the circular corpuscles of Man and other Mammals.

It thus appears that we may divide the blood corpuscles of animals into two classes, the nucleated and the non-nucleated. It must, however, be mentioned at once, that nucleated blood corpuscles occur at an early period of the development of the blood both in Man and Mammals.

Size of the Red Blood Corpuscles.—There is a large amount of literature bearing on the subject of the micrometric investigation of the blood.

The considerably differing results of the measurements that have been recorded have, for the most part, only a relative value. The micrometer employed has not, as a rule, been reduced to a definite standard. Exact comparison with a standard, it is well known, is no easy matter even for macroscopic measurement. But it is still more difficult in the case of the micrometer. Harting † and Welcker ‡ have, on this account, detailed special methods by which the measurement of blood corpuscles may be accomplished.

As a rule, only the size of those blood corpuscles should be compared, which have been obtained by the same observer with the same instrument. It is self-evident also, when all the foregoing remarks are fully taken into consideration, that only those measurements are serviceable for comparison, in which an exact statement is made of the conditions under which they have been made.

Hence, we must be on our guard respecting the inconsiderate employment of the various tables that have been published on the size of the blood corpuscles in different animals.§ The absolute dimensions obtained by Welcker‖ with a micrometer, are:—

* Donné, *Cours de Microscopie*, etc., Paris, 1843, p. 70; *Comptes Rendus*, T. xiv., p. 367.

† *Das Mikroskop*, etc., Band ii., p. 288, *et seq.*

‡ *Zeitschrift für rationelle Medicin*, 3 R., Band xx., p. 259.

§ The most extensive tables on this subject are to be found in Milne Edwards, *loc. cit.* p. 84.

‖ *Loc. cit.*, p. 263.

For man on an average expressed in millmetres :—

		Min.	Max.
Diameter of disk	0·00774	(0·00640	0·00860)
Greatest thickness of the disk	0·00190		

In six males and three females a minimum was observed of 0·0045 millimetre, and a maximum of 0·0097, all occurring between the terminal values, the smallest excepted, being very nearly of equal size.

The measurements were made on the corpuscles of fresh blood, or of blood dried in thin layers on glass.

The measurements given by Welcker for the small red corpuscles, described by Max Schultze, are 0·005—0·006 millimetre; and from these, gradual transitional forms may, according to Max Schultze, be traced up to those of ordinary diameter, from 0·008 to 0·010 millimetre.

We are indebted to Welcker for exact measurements of the corpuscles in various animals, and a few of his mean values will be found in the subjoined note.*

The smallest corpuscles are those of the Moschus Javanicus. Amongst the largest are those possessed by the perennibranchiate Proteus anguinus, and the Siren lacertina (the long diameter of which amounts to $\frac{1}{16}$ mm. and the short to $\frac{1}{30}$ mm.).† The largest known, according to Riddel,‡ are those of the Amphiuma tridactylum, which are one-third larger than those of the Proteus.

Welcker § employed a very short cylinder of plaster of Paris, the pro-

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* *Loc. cit.*, p. 279.

I. Circular Corpuscles.

Dog	0·0073
Cat	0·0065
Rabbit	0·0069
Sheep	0·0050
Goat (old)	0·0041
Goat (8th day)	0·0054
Moschus Javanicus	0·0025
Petromyzon mari	0·0150
Ammocœt branch	0·0117

II. Elliptical Corpuscles.

a, Long diameter; *b*, short diameter.

	a.	*b.*
Lama	0·0080	0·0040
Pigeon (old)	0·0147	0·0065
Pigeon (fledged)	0·0137	0·0078
Pigeon (fledged)	0·0126	0·0078
Duck	0·0129	0·0080
Fowl	0·0121	0·0072
Rana temporaria	0·0223	0·0157
Rana temp. (dry)	0.0214	0·0156
Triton Cristatus	0·0293	0·0195
Proteus (1 and 2)	0·0582	0·0337
	0·0579	0·0356
Sturgeon	0·0134	0·0104
Cyprinus Album	0·0131	0·0080
Lepidosiren Annectens	0·0410	0·0290

† Milne Edwards, *loc. cit.*, p. 89.
‡ *Journal de la Physiologie*, Band ii. Paris, 1859, p. 159
§ *Loc. cit.*, pp. 265–275.

portion of the radius to the height of which was estimated to correspond with the dimensions of the blood corpuscles; and by scooping out the surface, and rounding off the edge, he obtained a curvature of the surface, which, to the eye (!) was similar to that of the blood corpuscles (compare fig. 87). He thus determined the mean volume of human blood corpuscles to be 0·000,000,072,217 of a cubic millimetre. Welcker, moreover, carefully lined the interior of this model, which was 5,000 times larger than the corpuscles, with paper of uniform thickness, then weighed the paper used, and compared this with the weight of a known superficial measure of the same paper. From the data thus obtained he estimated that the superficies presented by a blood corpuscle amounts to 0·0,001,280 square millimetre. It is sufficiently obvious that these numbers have only a coarsely approximative value.

Number of the Red Corpuscles.

Estimates of the number of the corpuscles have also been undertaken with the microscope. This method was suggested by Vierordt, and has been modified by Welcker.*

Their direct enumeration may be accomplished in the following way:—

A measured volume of blood is diffused as equably as possible in a thousand times its volume of an indifferent fluid (six grammes of Na. Cl. in one litre of water, according to Welcker), a small quantity of the mixture is taken up in a capillary tube of known calibre, and the length of the thread of fluid is estimated under the microscope by means of a micrometer. When the contents of the tubule have thus been ascertained, they are quickly distributed with a little solution of gum upon a slide, and the whole is allowed to dry. The preparation is covered with a micrometer divided into squares, and the corpuscles in the several squares can then be successively counted. In one experiment Vierordt used 0·0005—0·0008 cubic millimetre of blood, in which about from 2,000 to 3,000 corpuscles were counted in the space of an hour.

Comparative enumerations, with test specimens of blood diluted to various extents, and measured in capillary tubes of various widths, gave a difference of two to three per cent. in the numbers, and seldom amounted to five per cent.

In a cubic millimetre of the healthy blood of a man, 5,000,000 red blood corpuscles were estimated to be present.

From this, and from the above-stated dimensions respecting the volume and surface of the corpuscles, there appear to be in a hundred volumes of blood thirty-six volumes of corpuscles and sixty-four volumes of plasma. The surface of the corpuscles in one cubic millimetre may be estimated to amount to 643 square millimetres.

Vierordt, Welcker, and Stölzing have also counted the blood corpuscles of various animals.

Alterations of the Red Blood Corpuscles.

We shall now pursue another line of inquiry. Up to the present time, independently of the above-given enumerations, we have, as far as possible, considered the blood corpuscles in their normal condition. We are, how-

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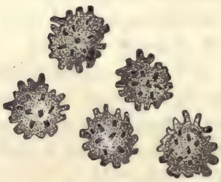
* Vierordt, *Archiv für Physiol. Heilkunde*, Band xi., pp. 26, 327, 854; xiii., p. 259; *Grundriss der Physiol.*, 3. Auflage, 1824, pp. 8, 9. Welcker, *Prager Vierteljahreschrift*, Band xliv., p. 60; *und Zeitschrift für rationelle Medicin*, 3 R., Band xx., p. 280.

ever, indebted for much important information to the observation of certain changes which the corpuscles undergo under various circumstances, as well as to the results obtained from experimental histology.

For the purposes of inquiry into the nature of the red corpuscles, mechanical agents, the discharge of the Leyden flask, the application of induced and constant currents, exposure to heat and cold, and lastly, the addition of various chemical agents have been employed.

1. In freshly prepared specimens of human blood it may frequently be seen, after the lapse of a variable space of time, that the borders and surfaces of the corpuscles have lost their smooth aspect. The borders appear dentated; the surfaces, as may best be seen when the corpuscles are rolling over, are beset with little eminences. At the same time the corpuscles become smaller and more spherical (fig. 89). A few such corpuscles are often visible in fresh blood, immediately after it has been drawn, so that it is difficult to determine whether they are pre-existent in it, whilst it is still circulating, or not. It is certain that, in blood abstracted from healthy persons, in many instances, nearly all the corpuscles undergo this alteration, and

Fig. 89.



this is stated (by Max Schultze) * to occur with still greater rapidity in those suffering from febrile diseases. The corpuscles thus altered have been described as mulberry-shaped, and the phenomenon regarded as a stellate contraction of the corpuscle. It was well known, long ago, to Hewson. †

The evaporation of water, and perhaps the cooling of the blood, are conditions favorable to these changes. But they may also occur, as will hereafter be shown, even when such conditions are not present. The appearances are presented by the corpuscles of Mammals, as well as by those of Man. And analogous phenomena are occasionally, though rarely, presented by the elliptical and nucleated corpuscles.

The blood corpuscles of Salamandra maculata, and of Triton crystatus and tæniatus easily assume a mulberry-like form under the microscope. In the blood of the Frog the phenomena first make their appearance as a consequence of the operation of external agents, and the corpuscles then become exactly similar to those of Mammals.

2. From the action of mechanical agents on the blood corpuscles we learn that their substance is composed of an extremely extensible and, within wide limits, completely elastic material.

That the blood corpuscles become elongated in their passage through the vessels, and that they also become curved in traversing the angles of division of the vessels, were facts well known to the older observers.

Lindwurm,‡ in thick solutions of mucilage; Hassall,§ in microscopic

* *Loc. cit.*

† *Opus posthumum*, pp. 19, 20.

‡ *Zeitschrift für rationelle Medicin*, Band vi., p. 266.

§ *Microscopic Anatomy*, p. 31, *et seq.*, plate ii., fig. 6.

coagula; and Henle,* in thick semi-fluid jelly, all saw the blood corpuscles assume a distorted or elongated and sometimes an extremely elongated fusiform shape.

The greatest variety of such forms is obtained when defibrinated blood is imbedded in pure solution of gelatine, melting at 35° to 36° C. (95° to 97° F.); from which, again, when it has become stiff, fine sections can be prepared, and placed under a covering glass; we may here particularly observe in such sections through the clefts of the gelatine, how the parts of the corpuscles drawn out into various forms, and often much attenuated, are always pale, and often even without perceptible color; whilst the swollen parts appear, on the other hand, more deeply tinted. Long processes extend from some of the corpuscles, which ultimately divide without coalescing with others. The nuclei of the elliptical blood corpuscles are somewhat less yielding, and they are frequently found to be completely detached from the substance of the blood corpuscles; these, however, in many instances, as is deserving of special mention, do not in consequence suffer any notable change, either in their diameter or in their capabilities of resistance.† Instances of the mechanical influences inducing change in the form of the red corpuscles occur, as already pointed out, in the movement of the blood while circulating. E. H. Weber,‡ in 1830, adduced his own observations upon this point, and referred to the numerous ones made previously to the time of Leeuwenhoek.

The phenomena may be well seen in examining the circulation in the membrane of the foot, and in the tongue or mesentery of the frog.

According to Rollett, in the circulating blood of Mammals, as, for instance, of guinea-pigs, that have been narcotized with opium, the red corpuscles of the blood do not retain their ordinary average form in the mesenteric vessels, when driven forward with the stream; but become, during their flow, more or less irregular in outline.§ If the current be retarded or altogether arrested, or if the blood corpuscles are compressed against each other, or against the interior of the vascular wall, they assume the same appearance as that which we have above described as characteristic of the fresh blood corpuscles. Moreover in diapaidesis, as it has been described from direct observation by Stricker, ‖ Prussak,¶ and others, the phenomena we are now considering may be observed in the red corpuscles during their transit through the vascular wall.

Lastly, it is to be observed that the blood corpuscles, notwithstanding their great extensibility, may be broken up by mechanical means.** This may easily be accomplished if a drop of fresh blood be quickly expanded into a thin layer by the pressure of a glass cover, which after the lapse of a few seconds is raised, and again firmly pressed down; there may then be seen colored spheroidal or discoidal fragments. In nucleated corpuscles, as in those of the frog and triton, isolated nuclei are often visible, which are usually round, frequently distorted, and always granular. The number of the colored fragments is always small in comparison with these, proving that the substance of the blood corpuscles becomes to some extent finely distrib-

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* Canstatt's *Jahresberichte*, 1850, Band i., p. 32.

† Rollett, *Sitzungsberichte der Wiener Akademie*, 1862, Band xl., vol i., pp. 65–71.

‡ *Handbuch der Anatomie*, Band i. Braunschweig, 1830, p. 159.

§ *Sitzungsberichte der Wiener Akademie*, Band l., p. 196.

‖ *Loc. cit.*, Band lii., p. 386.

¶ *Loc. cit.*, Band lvi., p. 13.

** Hensen, *Zeitschrift für wissenschaftliche Zoologie*, Band xi., p. 260. Vintschgau, *Atti dell' Instituto Veneto. Extr. dal* vol. vii., ser. iii., p. 3–6.

uted through, or actually dissolved in, the surrounding fluid, which in point of fact appears slightly tinted. In anticipation of observations hereafter to be mentioned, it must be specially remarked that in these researches no shrivelled colorless shreds were noticed representing remains of the broken-down corpuscles.

3. The characters presented by the blood corpuscles on drying also deserve mention. C. Schmidt* has observed that when a thin layer of blood corpuscles is dried upon glass, they remain extended, and do not undergo any remarkable change in the dimensions of their larger diameter. Welcker † and others have corroborated this statement. The clear spot of the non-nucleated corpuscles, to which alone the above statement is strictly applicable, comes, under these circumstances, very distinctly into view, but passes without sharp definition into the surrounding darker parts.

The nucleated corpuscles do not remain quite unaltered in the dimensions of their surfaces; the variation is, however, of small amount. Many retain their form and smoothness; others become curved or sinuous. The clear spot corresponding to the nucleus, and its delicate markings, come more distinctly into view. In some corpuscles the nucleus, after drying, always appears very sharply defined, and separated from the remaining substance of the blood corpuscles by a clear reddish refractile border investing it like a wall, and making it appear as if lying in a cavity. In blood dried in masses the blood corpuscles are found to present manifold changes of form and to become ultimately attached to one another, so that it is difficult to recognize them in frgments of dried crust.

4. In the coagula which originate in the lymph sacs of frogs or salamanders after bleeding, according to Rindfleisch ‡ and Preyer,§ colored or colorless processes are protruded from the substance of the corpuscles, which are at first smooth, but afterwards resemble a string of pearls. According to Preyer, these can be again withdrawn, or may become completely isolated, or may separate into a few spheroidal masses. Beale ‖ saw similar changes occur in the red corpuscles on a slide, in consequence of evaporation (? coagulation) and warming.

5. In order to observe the effect of electrical discharges¶ and of induction currents upon the blood corpuscles, the arrangement exhibited in pp. 14, 15, of this manual may be employed, except that it is better to provide the copper pole with clips than with hooks. In these the ends of the induction coil or the ends of a transversely divided discharging rod of a Leyden flask are received, so that the tin-foil electrodes make a complete arc of union with the blood found between them and the wires. In order to enter more minutely into the phenomena which can be observed under the microscope, it is necessary in the first instance to bear in mind the results of microscopic experiments.

If the blood of a mammal be introduced into the arc of discharge of a Leyden phial, and a series of shocks be passed through it, it becomes altered, losing its opacity, and assuming a transparent lake-like tint. Microscopic examination shows that the blood corpuscles become altered, ultimately presenting only extremely delicate, pale, and feebly refracting particles. If

* *Die Diagnostik verdächtiger Flecke.* Mitau and Leipzig, 1848, p. 3, *et seq.*
† *Loc. cit.*, p. 261.
‡ *Experimental Studien über die Histologie des Blütes.* Leipzig, 1863, p. 8.
§ Virchow's *Archiv*, Band xxx., p. 417.
‖ *Quarterly Journal of Microscopical Science*, No. 13, 1864.
¶ Rollett, *Sitzungsberichte der Wiener Akademie*, Band xlvi., pp. 92–97; Band xlvii., pp. 356–390; Band l., pp. 178–202.

in a consecutive series of examinations the number of the discharges requisite to produce the most complete transparency possible be taken as a measure of comparison for the clarifying power of the discharging current, we arrive at the following conclusion:—

The action of each successive shock is superadded to those which precede it.

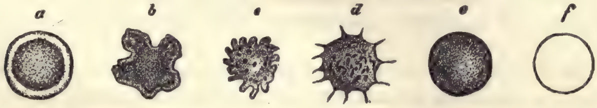
The transparency of each element of the conductor formed by the blood is dependent on the intensity (density) of the current acting upon the unit of its transverse section with which it proportionally increases; it is also dependent upon the amount of what may be termed the specific resistance of the blood corpuscles, which differs in different kinds of blood, and with the increase of which, though not in a hitherto clearly ascertained ratio, the clarifying influence diminishes.

With a given specific resistance of the blood corpuscles, and with given size and specific conductivity of the blood, the course of the phenomena can be varied according to the quantity and mean intensity of the electricity in the phial.

The most advantageous distance of the tin-foil electrodes from one another for microscopic investigations is six millimetres; between these a thin layer of blood, covered with a thin plate of glass, should be introduced, and a Leyden flask employed, presenting a surface of about five hundred square centimetres, with a striking distance of one millimetre. Striking distances of greater extent cannot be used, as the blood with the glass cover may be easily displaced, the sparks then passing directly from one electrode to another. Moreover, the surface of the flask must not materially exceed the above, or the discharging shock will occasion electrolysis (scarcely perceptible in the above-mentioned arrangement) to occur to an extent which may seriously interfere with the result. When these conditions are preserved, and the discharges are made to succeed each other at intervals of from three to five minutes, the following consecutive changes may be observed in the blood corpuscles:—

The circular disk-like corpuscles (fig. 90, *a*) in the first instance present one or two projections at their borders, and these gradually increase in number to three, five, or more.

Fig. 90.



I have named this form the rosette form (fig. 90, *b*); it passes gradually into the mulberry form (fig. 90, *c*), which can always be produced at will by the discharge. To this succeeds a stage in which the processes become pointed, so that the corpuscles assume more the form of a paradise apple (horse chestnut) (fig. 90, *d*). Lastly, all the spikes are withdrawn, and a colored corpuscle results (fig. 90, *e*), which then loses its color, and a smooth colorless body is left (fig. 90, *f*), that long remains in the fluid in an unaltered condition.

In the case of the frog the blood corpuscles first assume a spotted appearance. Local thickenings then occur in the direction of the shortest diameter, which for the most part proceed radially from the nucleus (fig. 91, *a* and *b*). This, however, is not always the case; for it sometimes happens that

the thickenings are nearly perpendicular to the longest diameter of the corpuscle, and cross it in the form of transverse bands. The latter is of most frequent occurrence in the blood of tritons. Upon this stage, which is obviously analogous to the first (fig. 90, *b*) and to the second (fig. 90, *c*) stage in the blood corpuscles of Mammals, there follows a stage in which the corpuscles again become smooth; their substance is then equably thickened, but the two other diameters have become somewhat smaller, whilst the mass either on one or both sides of the nucleus becomes swollen, so that the latter, as it were, closes a communication between the halves of a double funnel. At length the walls of these funnels coalesce, and the corpuscles be-

Fig. 91.

come egg-shaped or round. In the latter condition they are at first still colored, but at a later period they gradually lose their coloring material, and there then only remains a dull colorless mass surrounding the nucleus. The nuclei appear somewhat rounded and more clearly visible in their interior.

Just as the coalescence of corpuscles may be observed to occur at the points where they are accidentally in contact, so it frequently happens that two or more blood corpuscles, when they have become colored spheroids, completely coalesce with each other. The largest spheroids with numerous nuclei then lose their coloring matter just in the same manner as the individual corpuscles. Another highly remarkable phenomenon is that the nucleus may escape suddenly or gradually from the corpuscles. Non-nucleated colored spheroids thus originate, which again gradually lose their color. Neumann also has subjected the operation of induction currents upon the blood corpuscles to examination, and the phenomena he has observed agree in all essential particulars with those that have been above described.

On the other hand, the constant electric current does not produce these effects. It only produces alterations in the blood corpuscles in the immediate neighborhood of the metallic electrodes; those observed at the positive pole being similar to those effected by acids, and those of the opposite pole to those of the alkali which is there set free.* We shall hereafter enter more fully into the action exerted by acids and alkalies on the corpuscles.

6. After Klebs,† Rollett,‡ and Beale § had originally described the influence of increased temperature on the red blood corpuscles, Max Schultze ‖

* Rollett, *loc. cit.*, Band xlvii., p. 359; Band lii., p. 257. A. Schmidt, Virchow's *Archiv*, Band xxix., p. 29; *Hämatologische Studien.* Dorpat, 1865, p. 116. Neumann, Reichert and Du Bois' *Archiv*, 1865, pp. 682–690.

† *Centralblatt für die medicin. Wissenschaften*, 1863, p. 851.

‡ *Loc. cit.*, Band l., p. 192.

§ *Loc cit.*

‖ *Loc. cit.*, p. 1.

first applied a more exact and methodic mode of investigation by means of the slide he has constructed, which is capable of being heated to a definite degree.

At about 52° C. (125° F.) the red corpuscles of man present first shallow and then deep fissures, which ultimately lead to the detachment of spherical masses. Some blood corpuscles assume various shapes, or thrust forth moniliform fibres. The latter forms immediately remind one of those found by Rindfleisch and Preyer in extravasated blood. Finally, spheroidal colored drops are always found, so that the middle part of the original corpuscles corresponds to one of the larger of such fragments, which, varying in magnitude from this to an almost molecular fineness, are beset with smaller particles at their margin, or are surrounded by a series of them in a free state. The alterations described by Klebs as occurring at a temperature of 38° C. (100° F.) were not observed by Max Schultze. From observations made in a water bath, Rollett ascertained the temperature at which the blood corpuscles became spheroidal to be between 40° and 50° C. (104°—122° F.) The changes in the corpuscles, however, do not occur suddenly, but only after long exposure, and without the segmentation observed at 52° C. (125° F.)

Lake-colored blood, according to Max Schultze, is first obtained when the temperature is raised to 60° C. (140° F.)

At about 53° to 54° C. (127° to 129° F.), Max Schultze observed the same changes in the blood corpuscles of the fowl as those that have been already described.

The corpuscles of the blood of the frog at about 45° C. (130° F.) become partially maculated and to some extent tuberculated on their surface, others assume the form of a finger-biscuit or of a dumb-bell, whilst a few become oval or spherical.

7. If blood, contained in a platinum vessel, be alternately frozen and thawed several times in succession, it likewise assumes a carmine color.

The non-nucleated blood disks are deprived of color without becoming materially diminished in size, or they will be found to have become spherical, or of smaller diameter, or only their feebly refracting colorless remains can be discovered.

In the corpuscles of the blood of the frog the nucleus is seen to be surrounded by a pale elliptical or circular area, or the color of the blood corpuscle appears to be to some extent retained. Various forms are also found which appear indented or chipped off; finally, here also the blood corpuscles lose their color.

The extensibility and elasticity of the uncolored remains of the blood corpuscles are similar to those of the intact blood corpuscles.*

In frozen blood the nuclei either still resemble unaltered nuclei, only somewhat more sharply defined, or they are spheroidal, enlarged, and appear as if composed of a delicate framework of highly refractile substance, in the meshes of which a less strongly refractile substance is contained. These spaces are often but few in number. Frequently only a single space is present in the form of a large vacuole surrounded by a ring of refractile material. These characters of the nucleus deserve attention in regard to facts that will hereafter have to be mentioned.

8. In reference to the phenomena that are occasioned by the addition of fluids to the blood corpuscles, three different conditions under which they may occur must be clearly distinguished. The reagent may be intimately

* Rollett, *loc. cit.*, Band xlvi., pp. 74, 75.

commingled with the blood by mechanical means, in which case it is only possible to observe the final changes effected in the corpuscles by the reagent under the microscope; or the plasma or serum of the blood corpuscle may be washed away with the reagent, under the microscope, in the manner described at p. 13. of the introduction to this work, in which case, in order to prevent the corpuscles from floating off, it will be found advantageous to spread upon the slide a thin layer of a felt-like mass of fine clean asbestos, or of scraped Swedish filtering paper, and to place the blood drop on this; or, lastly, the blood and the reagent may be placed in close proximity with each other, and allowed to diffuse slowly.

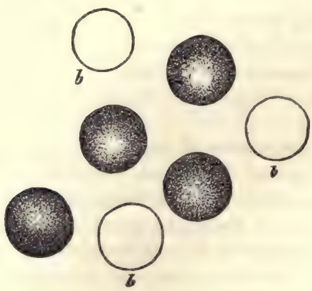
It is only when, in the process of washing by the first method, the several blood corpuscles exhibit differences in their behavior with the reagent that we are justified in concluding that an internal and original difference exists between them.

It is not permissible to draw this conclusion when the second and third methods are employed, or at least only providing that very great caution has been exercised; for if the uniformity of the mixture has not been constantly maintained, some of the corpuscles will necessarily be first and more energetically acted on by the reagent, and the amount of change in any instance will be proportionate to the duration of the exposure to its influence. We may very easily satisfy ourselves that the changes effected by one and the same reagent are very different during the first period of its action, and lead to other results than at later periods.

The many difficulties that encompass the study of the operation of reagents on the blood have not, as a rule, received sufficient attention; and less, perhaps, has been accomplished by this mode of experiment than might otherwise have been the case.

a. The addition of water renders the surface of the corpuscles smooth, and so changes their various diameters that they become spherical,* and thus acquire that form which with a given surface can contain the largest amount of material. This effect is commonly indicated as a process of imbibition, a

Fig. 92.



swelling up, although the diameter of the spheroid may be actually smaller than the long diameter of the corresponding disk (fig. 92). The spheroids are at first strongly colored. On the cautious addition of water it may be frequently observed that the alteration of the primary form of the blood corpuscle to a spheroid does not occur with perfect uniformity in all the several and corresponding diameters, so that variable and transitory unsym-

* Hewson, *Opus posthumum*, p. 25.

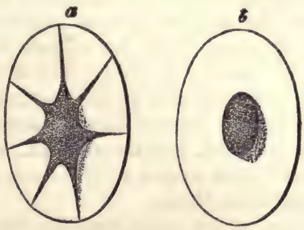
metrical intervening forms are met with. In the nucleated ellipsoids it frequently happens that the nucleus changes its position in the corpuscle with a jerk,* whilst the corpuscle itself, as though in consequence of a recoil, is projected in the opposite direction. The nucleus then lies eccentrically in the corpuscle.

When water has continued its action on the corpuscles for a longer period, the spheroids become discolored, and frequently produce the impression that their coloring matter is being gradually extracted; frequently also the color disappears very rapidly, just as a hue of color vanishes from a white surface when a colored source of light by which it was previously illuminated is suddenly removed. The impressions thus given are precisely similar to those decolorations which have been formerly mentioned as the result of electrical discharges.

Smooth colorless bodies with feebly defined but smooth contour lines then remain (fig. 92, *b b b*).

The nucleus which at the commencement of the action of water, when the corpuscles have acquired a spherical form, comes more prominently into view, and remains so as long as these still retain their color, but subsequently becomes less conspicuous, and after the long operation of large excess of water appears smooth, distended, and less highly refractile.

Fig. 93.



Especial attention should be directed to a structure which can be easily demonstrated in the elliptical corpuscles after the cautious addition of water (fig. 93). The still ellipsoidal corpuscle is bounded by a perfectly smooth contour line, but the place of the nucleus sometimes appears to be occupied by a colored spheroid; whilst in other cases numerous processes radiate from this ball towards the contour line, becoming pointed peripherically. The parts lying between the latter and the colored portion are homogeneous and colorless.

According to Kneuttinger,† these forms are obtained when fresh frog's blood, from which the fibrin has not been removed, is mingled with three or four times its volume of water, and an examination shortly afterwards made of the gelatinous mass.

If larger quantities of water be added and thoroughly commingled with the blood, some of the corpuscles remain much longer in the condition of colored spheroids than others; and the inference has been not unreasonably drawn, that an essential difference exists amongst such corpuscles.

b. Salts act very differently, according to their chemical nature and their degree of concentration. Many metallic salts occasion precipitates

* See also the statements respecting the movements of the nucleus by C. H. Schultz. Preyer, *loc. cit.*, p. 437.

† *Zur Histologie des Blutes.* Würzburg, 1865, p. 21.

in the blood corpuscles similar to the acids hereafter to be mentioned. The action of those salts which produce no precipitate (common salt, Glauber's salt, sal ammoniac, borax, magnesium chloride, and others) has been repeatedly described, in contrast to the action of water, as a shrivelling or contraction. Solutions of this nature cause the blood corpuscles to become less glutinous and extensible, their outline more distinct, their form curved, their surface wrinkled, and their border dentated. Such are the effects of moderately strong solutions of these salts. Very strong solutions of some of these salts, or the addition of the salts themselves, in powder, to the blood (common salt, Glauber's salt, magnesium chloride), only cause the blood corpuscles to shrink in the first instance, but soon they become round and pale, so that only colorless bodies remain.* In dilute solutions of some of these salts, the concentration of which is about equal to that of the blood serum, the corpuscles retain their characters for some time without alteration. Solutions of this kind are therefore frequently applied instead of serum for the purposes of dilution. With still greater degrees of dilution effects are produced similar to those that are observed when water is added in quantity to the blood.

A successive series of forms may frequently be observed to occur in the nucleated elliptical blood disks on the addition of saline solutions of medium degrees of concentration, though they cannot be certainly caused to appear. Hühnefeldt and Hensen† have obtained and represented forms similar to those above mentioned, by the agency of ammonia and sal ammoniac. They may also be observed on the applications of other saline solutions. They are almost identical with those that have been already described as resulting from the action of water (fig. 93). The blood corpuscles, however, appear equally maculated, colored and colorless areas alternating with regularity; or, as frequently occurs in the blood corpuscles of Tritons, on the addition of three or four per cent. solutions of common salt, projections may form on the flat surface at right angles to the long axis, with paler or colorless spaces intervening between them.

The alkaline salts of the biliary acids, and the bile itself, according to the older observations of Plattner (1844), which Kühne‡ has corroborated by more recent researches, dissolve the red corpuscles of most animals, with phenomena in those of man which are similar to the effects that, according to L. Hermann, result from the action of chloroform or ether on the corpuscles. This subject, however, will be more fully discussed hereafter.

c. The action of sugar under the microscope is similar to that of the above-named salts. Its solutions, in moderate degrees of concentration, harden the corpuscles by the withdrawal of water, and forms are produced analogous to those that are met with after the action of moderately strong alkaline solutions.

d. Alkalies,§ as a general rule, when in a state of moderate concentration, exert a solvent action on all the constituents of the blood corpuscles, including the nuclei. The following may be particularly mentioned amongst the many forms that are met with :—

* Kölliker, *Zeitschrift für wissenschaftliche Zoologie*, Band vii., p. 184. Botkin, Virchow's *Archiv*, Band xv., p. 176. Bursy, *Ueber den Einfluss einiger Salze auf die Krystallisation des Blutes*, "On the Influence of some Salts on the Crystallization of the Blood." *Inaug. Diss.* Dorpat, 1863.

† *Zeitschrift für wissenschaftliche Zoologie*, Band ix., p. 261.

‡ Virchow's *Archiv*, Band xiv., p. 333.

§ Kneuttinger, *loc. cit.*, p. 39.

In the case of potash and soda lyes, and of solutions of lime, baryta, and strontian, containing 0·1 gramme in 100 cubic centimetres of water, a remarkable difference occurs, as compared with the action of pure water; for the corpuscles first change into colored spheroids, but soon disappear without leaving a trace. In the nucleated blood corpuscles, on the other hand, after they have become converted into colored spheroids, the nucleus may still be indistinctly seen, and appears to be expanded in its interior, though the diameter of the colored spheroid is not itself materially altered. The corpuscle soon gives the impression of undergoing flattening, and immediately the whole spheroid, with the nucleus, entirely disappears. As already stated, the impression of the flattening occurs only in the nucleated blood corpuscle, but is visible both in the elliptical corpuscles and in the nucleated round corpuscles of the embryos of Mammals. If the action of the reagent penetrating into the blood be rendered less energetic, the flattening still often occurs; and when all the rest of the corpuscle has quietly dissolved, the nucleus remains behind, enormously enlarged, and usually of a somewhat angular form, though homogeneous in its substance. This phenomenon, however, may be more frequently observed after the application of the alkaline earths than after that of the pure alkalies. In regard to lime-water, it deserves especial mention that, in many instances, after the colored spheroids have been produced, and the corpuscles are about to flatten, the previously enlarged nucleus contained in the interior of the spheroid contracts suddenly to a strongly refracting body. The corpuscle then becomes pale, and this centrally situated body remains surrounded by a clear colorless area. This peculiar appearance occurs usually only at the commencement of the action of lime-water.

e. Acids * readily occasion precipitates in the blood corpuscles. The precipitate either appears distributed through a clear transparent substance, surrounded by the circular or elliptical contour line of the corpuscle, which frequently expands suddenly with a jerk (acetic acid); † and coincidently the nucleus, which has become more highly refractile, and frequently somewhat angular or inflated, and darkly granular, comes more distinctly into view (acetic acid, diluted tincture of iodine), whilst it appears distinct from the colorless substance of the blood corpuscles, in consequence of being strongly tinted with hæmatin; or the precipitate occurs in the thoroughly granular or cloudy corpuscle, which appears as if hardened and usually somewhat shortened in its long diameter. When the acids act in this manner, the nucleus frequently appears to be not very sharply defined, but frequently shrivelled and surrounded by an empty space, as though lying in a cavity of the substance of the blood corpuscles (chromic acid, hydrochloric acid, nitric acid, picric acid, tannic acid, and concentrated tincture of iodine). When the acids are much diluted, the second of the above-mentioned modes of operation frequently passes into the first, because in very diluted acids the action of the acid is complicated with that of the water.

The former of the above-mentioned effects is best exhibited by means of acetic acid, in solutions containing twenty grammes of pure acetic acid in 100 cubic centimetres of water, and upwards. The beautiful staining of the nucleus, with the coloring matter of the blood, which then occurs, was first mentioned by Henle,‡ and has been corroborated by Kneuttinger; § it is

* Kneuttinger, *loc. cit.*, p. 28.
† *Idem.*
‡ *Allgemeine Anatomie*, p. 431.
§ *Loc. cit.*, pp. 28, 29.

exhibited in the most beautiful and convincing manner if the blood of a frog or triton is allowed to float into acetic acid: the blood sinks in the acid, and the dregs of the vessel can then be examined.

The non-nucleated corpuscles of Man and Mammals are first rendered spherical by the action of acetic acid, and then lose their color, in which condition they remain for a considerable period.

Brücke * has subjected to a special investigation the changes that are effected on corpuscles of the fresh blood of the triton by the action of a two per cent. solution of boracic acid, and we shall now proceed to describe them. Soon after the addition of the solution the corpuscles seem to be converted into ellipsoids, as after the action of certain proportions of water, the nuclei being often eccentrically situated; they ultimately, to a greater or less extent, become spherical. Forms are also obtained similar to those that have already been mentioned as occurring after the addition of water or saline solutions (fig. 93). In other corpuscles the nucleus alone appears of a deep color, the remaining substance of the corpuscle being pale or completely colorless, and separated by a smooth contour line from the surrounding fluid, as after the action of many other acids in certain degrees of dilution. Direct observation of the action of boracic acid under the microscope renders it evident that the latter form does not necessarily proceed from any of the foregoing. In the greater number of instances the nucleus gradually becomes colored, without the color being discharged from the border of the corpuscle, although the substance of the corpuscle becomes proportionately colorless. A similar coloration of the nucleus occurs also with a two per cent. solution of boracic acid, when applied to the corpuscles dried on a slide. If the corpuscles are so modified by freezing, by shocks of electricity, or by ether or chloroform (the changes effected by which will be subsequently considered) that they have yielded up their coloring matter completely to the serum, and they are then treated with a two per cent. solution of boracic acid, the nuclei still acquire their deep tint from the coloring matter contained in the surrounding fluid. Brücke also observed the corpuscles discharge their nuclei from the action of boracic acid.

f. If it be desired to ascertain what alterations are effected in the blood corpuscles by small variations in the degree of acidity or alkalinity of the reagent, it is requisite, as has been shown by W. Addison,† in order to avoid the action of the water of the solution, to give a certain degree of concentration to the fluid by the addition of a small proportion of sugar or of salt. In such investigations it will be found, as he has correctly stated, that on the addition of an acid fluid, as of a solution of cane sugar weakly acidified with hydrochloric acid, the blood corpuscles possess, in all instances, smooth contours, and exhibit an increased degree of refraction; whereas on the addition of an alkaline fluid, as of a solution of common salt rendered feebly alkaline with liquor potassæ, the blood corpuscles become granulated and rough.

Appearances essentially similar are produced with still greater clearness by passing weak currents of electricity through the blood. That the corpuscles quickly become tuberculated and spinous in the vicinity of the alkaline pole was observed by Neumann,‡ who also saw the formation of the fibres described by Addison.

The change of form corresponding to the action of weak alkalies can, ac-

* *Sitzungsberichte der Wiener Akademie*, Band lvi., p. 79.

† *Quarterly Journal of Microscopical Science*, 1861; Jan., *Transact.*, p. 20; April. *Journal*, p. 81.

‡ *Loc. cit.*, pp. 679—681.

cording to Addison, be changed by acid solutions into the form they induce, and *vice versâ*.

g. Urea,* in the state of fine powder, or in solution in water, in the proportion of from twenty-five or thirty grammes or less in 100 cubic centimetres of water, powerfully affects the form of the corpuscles, though they are not all affected in the same way.

In the blood of Amphibia some of the corpuscles always assume a curved form, and then small drops and spherical fragments become detached from them. Others become spherical without undergoing any further alteration in shape; but both large and small spheroids ultimately become colorless. During the assumption of the spheroidal form some of the corpuscles discharge their nuclei. The latter become slightly enlarged in the Frog, but much augmented in volume in the Triton, and then assume the remarkable appearance of a trabecular framework with large meshes. The nuclei which do not escape undergo similar changes if once the spheroid become colorless, so that the pale clear remains of the substance of the blood corpuscles appear as a kind of appendage to the enlarged nucleus. To regard these structures as nucleated albuminous spheroids escaped from adjoining colored corpuscles is due to a misconception of the phenomena observed.†

If we now consider the action of less concentrated solutions of urea, we find that the incurvation of the corpuscles and detachment of drops is of rarer occurrence, and that the majority of corpuscles immediately become spherical, and at a subsequent period, together with the nucleus, entirely vanish. The incurvation of the border and the formation of drops is also exhibited by the non-nucleated blood corpuscles of Mammals when treated with urea.

h. Neutral solutions of carmine in pure ammonia (one gramme of carmine in 200 cubic centimetres of solution) produce on the corpuscles the same effect as water. In the blood of Amphibia the inflated nuclei become, after a short time, tinged of a red color. The blood corpuscles behave differently in the above-mentioned solutions of carmine in ammonia if from one-half to one per cent. of common salt be added, since they then remain apparently unaltered, and take up none of the carmine into their interior. On the other hand, the nucleus immediately becomes stained. If a mixture of blood and this colored saline solution be allowed to freeze or be acted on by discharges of electricity, a series of remarkable phenomena may then be observed, upon the investigation of which I am now engaged.

If the blood of frogs or newts be allowed to flow into such saline solutions of carmine, there may always be found, besides the ordinary red and white blood corpuscles with nuclei, which long remain unstained, a few isolated free nuclei of an intense red color. It thus appears that when unaltered the blood corpuscles do not absorb any coloring matter.

Rindfleisch‡ has described a remarkable alteration effected in the blood corpuscles of the frog by the addition of soluble anilin blue. They are then found to become nucleated spheroids, which quickly assume a blue color, but it is only in solutions containing about a half-gramme to 100 cubic centimetres that the remarkable phenomenon of the discharge of the nucleus from the now spherical corpuscles occurs. It is especially remarkable that any part of the nucleus which once projects beyond the contour line of the cor-

* Hühnefeldt, *Chemismus in der thier. Natur.*, 1840, p. 60. Kölliker, *Zeitschrift für wissenschaftliche Zoologie*, Band vii., pp. 184, 253. Botkin, Virchow's *Archiv*, Band xx., p. 37. Hensen, *loc. cit.*, p. 264. Vintschgau, *loc. cit.*, p. 13. Preyer, *loc. cit.*, p. 432. Kneuttinger, *loc. cit.*, p. 56.

† Kneuttinger, *loc. cit.*, p. 58, fig. 9 *b*.

‡ *Loc. cit.*, pp. 10, 11.

puscle immediately swells up to a considerable extent, so that at this period the form of the nucleus resembles a short nail with a large head, which seems to have been driven into the substance of the corpuscle. When the nucleus has become altogether detached from the corpuscle, it swells up uniformly, becomes stained, and undergoes further changes, to be hereafter investigated.

i. Gases and vapors have lately, since the employmeut of gas cells, been likewise applied directly to preparations of blood under the microscope.

a. Stricker* has been especially engaged in investigating the action produced by the exposure of the blood corpuscles of the newt and frog alternately to carbonic acid and air.

So long as the blood remained unchanged he observed only the already-mentioned phenomena in the micro-spectrum, and was thus enabled to correct the older inexact statements.† Blood corpuscles changed by the action of water, however, behaved themselves differently.

Stricker applied water in the form of vapor, by which means very fine gradations in the amount supplied can be attained.

On transmitting carbonic acid he then observed the occurrence of precipitates both in the nucleus and in the substance of the corpuscle; these precipitates vanished with oxygen, and returned with carbonic acid, and so on. Stricker considers these appearances, as had already been held by A. Schmidt and Schweigger-Seidel in the case of the precipitate obtained by the action of carbonic acid in the substance of the blood corpuscles of the frog, to be caused by the separation of paraglobulin; in order, however, to obtain such precipitates the addition of water must be carried almost to the extent of rendering the blood corpuscles colorless.

If smaller quantities of water be added, these precipitates do not occur. Under certain conditions the remarkable form appears that we have already described (fig. 93, *a*). This form, as an easily repeated experiment of Stricker shows, vanishes with an excess of carbonic acid. The blood corpuscles then appear once more equably tinted, and on the admission of air revert again to their original form.

With the addition of a certain amount of water the nucelus alone becomes tuberculated, and more sharply defined when carbonic acid is transmitted, whilst upon the passage of air it again becomes smooth. If this stage be exactly attained, the whole blood corpuscle may be seen to become spherical with carbonic acid, and again to assume its smooth form on the admission of air. Moreover, the thorn-apple form of the mammalian blood corpuscles can be made to disappear by carbonic acid, but can again be produced on the accession of air; the experiment, however, as Stricker has remarked, cannot be very frequently repeated, as the thorn-apple form ultimately remains persistent. A. Schmidt‡ showed that ozone gave a carmine tint to the blood by destruction of the blood corpuscles.

b. Ether,§ chloroform,‖ bisulphide of carbon,¶ and alcohol,** conducted

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* Pflüger's *Archiv*, 1868, p. 590.

† Harless, *Monographie über den Einfluss der Gase auf die Form.* Erlangen, 1846. "Monograph on the influence of gases on form."

‡ Virchow's *Archiv*, Band xxix., p. 14.

§ V. Wittich, *Journal für praktische Chemie*, Band lxi., p. 11; and *Königsberger Medic. Jahrbücher*, Band iii., p. 332. L. Hermann, Reichert and Du Bois' *Archiv*, 1866, p. 27.

‖ Chaumont, *Monthly Journal of Medicine.* Edinburgh, 1851, p. 470. Böttcher, Virchow's *Archiv*, Band xxxii., p. 126; Band xxxvi., p. 342. Kneuttinger, *loc. cit.*, p. 48. A. Schmidt and Schweigger-Seidel, *Berichte der König. Sächs. Gesellschaft der Wissenschaften*, 1867, p. 190.

¶ Hermann, *loc. cit.*

** Hermann, *loc. cit.* Kneuttinger, *loc. cit.*, p. 44.

in the form of vapor over the blood, also render it of a carmine color. If the appearances exhibited by the blood corpuscles are closely observed, it may be seen that in the circular disks the border becomes thickened,* and in place of the central depression a navel-like fossa appears. The funnel so formed becomes narrower and closes, and the corpuscles now appear as a colored spheroid. Chloride of methyl vapor acts in a similar manner.† The above-mentioned vapors, but not the last, finally render the corpuscles colorless.

When ether and chloroform vapors act on the blood of the Amphibia, they render the corpuscles, in the first instance, spotty, though the color subsequently becomes equably diffused, whilst the blood corpuscles appear to be somewhat diminished in size. On the other hand, the thickness of the border is increased, so that the nucleus lies in a depression. A few only of the blood corpuscles become spherical. The majority, when in the condition of a disk with thickened borders, lose their color, and the nuclei then become more sharply defined. The blood corpuscles of the Amphibia also behave themselves similarly when air impregnated with ether or chloroform vapor is persistently transmitted over the preparation, and the phenomena do not essentially vary if the air thus charged with vapor is exchanged at definite periods for pure air.

If these reagents be added to the blood in a fluid condition, it will be found that ether and chloroform effect similar changes, except that a large number of blood corpuscles become spheroidal. Alcohol readily produces precipitates and irregular shrivelling.

OPINIONS RESPECTING THE STRUCTURE OF THE RED BLOOD CORPUSCLES.—In the exposition of these we need only go back to the time when the view which, though it had been advanced indeed before Schwann, yet was generally adopted only in consequence of his doctrine of the structure of animal cells, namely, that the red corpuscles are vesicles consisting of a membrane with fluid contents, began to be doubted.

The opponents of this view, after Max Schultze had, in 1861, demonstrated that a cell membrane is not a constant constituent of a cell, directed their attacks against the presence of a membrane in the red blood corpuscles. The presence or absence of a membrane must necessarily influence the conception of the nature of those constituents of the blood corpuscles which were formerly regarded as the colored contents. In the criticism directed by Max Schultze against the cell theory of Schwann, the red blood corpuscles played a part, since in the discussion respecting the necessity of a nucleus to complete our idea of a cell, those of Man and Mammals were adduced as being destitute of a nucleus. This was for a considerable time almost universally taught, and of late has been opposed by Böttcher ‡ alone. After what has already been stated in reference to the question of the nucleus, however, I do not consider it requisite to enter more fully into that subject, but shall refer to the communications of Böttcher, Klebs, § A. Schmidt, and Schweigger-Seidel.‖ We must deal differently with the question, whether the red blood corpuscles do, or do not, possess a membrane.

It must, I think, in reference to this point, be admitted that important

* Hermann, *loc. cit.*, p. 31. A. Schmidt and Schweigger-Seidel, *loc. cit.*, p. 196.
† Hermann, *loc. cit.*
‡ Virchow's *Archiv*, Bände xxxvi. and xxxix.
§ Virchow's *Archiv*, Band xxxviii.
‖ *König Sächs. Gesellschaft*, etc., *Math. Phys. Classe*, 1867, p. 190.

evidence, based on the form of the corpuscles, can be adduced against the view that they consist of vesicles in the sense held by a large number of histologists after the time of Schwann.

A vesicle filled with fluid, the parietes of which are yielding, and which again floats freely in another liquid, might be conceived to assume almost any form rather than of a body with two concave surfaces, as in Mammals, or with two convex surfaces, surrounded by a circular or elliptical zone of a certain thickness, as in Birds, Amphibia, and Fishes.

Schwann * adduced the assumption of a spheroidal form by the blood corpuscles on the addition of water, as a proof of their vesicular nature, maintaining that if they were not so they might indeed swell up and become colorless, but that they would retain their form like a sponge on the imbibition of fluid. The explanation of the action of water producing tension of the membrane, in consequence of the fluid contents of the vesicle increasing by endosmose, was at this time very generally accepted, just as the shrivelling of the surface, on the addition of saline solutions, was regarded as a consequence of a diffusion current setting from the interior. Brücke,† however, showed that neither the phenomena presented by the imbibition of water, nor after the addition of saline solutions, furnished conclusive evidence of the vesicular nature of the corpuscles.

If we base our opinion on the experiments performed on the red blood corpuscles by means of mechanical agents, we may exhaust all the various methods, without once meeting with a form which can be indisputably regarded as the torn and empty investing membrane, and the occurrence of which is in no other way capable of being explained; so again, whatever may be the changes that induction currents and electrical discharges, as well as freezing, induce in the corpuscles, no condition can at any time be seen directly proving the presence of a membrane.

On the contrary, the escape of the nucleus, the coalescence of the colored spheroids, the physical character of the colorless remains after the discharge of the coloring matter, are all opposed to the existence of such an investment. The results of these inquiries are much more in favor of the view maintained by Rollett,‡ that a stroma or matrix enters into the structure of the colored elastic extensible substance of the red blood corpuscles, which exhibits so remarkable a similarity in all animals, and that to this the form and the peculiar physical properties of the corpuscles are due. Hence the conclusion, that, however complicated the chemical constitution of the substance of the blood corpuscles may be, yet, by the action of a series of agents, the coloring matter can be separated from the stroma, without causing the latter to lose its essential characters.

The phenomena induced in the red blood corpuscles by various reagents, as urea, chloroform, and ether, and also the phenomena described by Max Schultze as resulting from the action of heat, fairly agree with this simple view. No doubt it may be urged that the membrane is highly extensible, and that it is reasonable to suppose that by the action of the above-mentioned agents it would be rapidly destroyed, rendering the phenomena observed consistent with its original presence around the tenacious semi-solid gelatinous contents of the blood corpuscles. But the theory that under these circumstances the membrane is really destroyed can only be based on the proof

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* *Ueber die Uebereinstimmung in Structur und Wachsthum der thierischen und Pflanzlichen Organismen.* Berlin, 1839, p. 74.

† *Berichte der Wiener Akademie*, Band xliv., p. 389.

‡ *Loc. cit.*, Band xlvi., pp. 73, 94, 95, and 98.

of its existence. We cannot hold the latter as ascertained if we regard the forms which a series of reagents (acids) occasion in the blood corpuscles; in the latter case we have much more ground for believing in the formation of artificial products, than they who hold the opposite view have reason in the previously adduced cases to admit the destruction of a naturally present membrane. The proof of the pre-existence of a membrane must here again, in the first instance, be furnished.

A circumstance bearing upon the question of a membrane is met with in the peculiar structures already frequently mentioned as occurring in the blood corpuscles of the Amphibia (Fig. 93, *a b*). A retraction of the cell contents from the membrane has here been considered to occur, and we may associate with this the forms which Remark * and more recently Preyer † have described in regard to the fission of blood corpuscles, in which a gradually deepening furrow detaches a colored portion of the blood corpuscle, whilst a glass-clear substance (the empty membrane) becomes apparent between the separating part and the investing contour line of the rest of the corpuscle.

Hensen, ‡ who has devoted considerable attention to the first-mentioned forms, sought to explain the retraction of the contents from the membrane, the existence of which he believed, from his observations of these forms, to be proved, by ascribing a protoplasm to the red blood corpuscles, which invests the nucleus and lines the inner surface of the membrane (primordial utricle), these two portions being connected by delicate radially coursing fibres, in the spaces of which the closed cell fluid is contained; he supported this view especially upon the existence of colorless fibres running in a radial direction from the nucleus, and it is well known that similar observations have been made by other histologists. But, independently of these fibres, which certainly do not represent any constant structure in the blood corpuscles, since they only appear to be met with under exceptionally favorable circumstances, the protoplasm distributed throughout the whole corpuscle must, according to the view of Hensen, form a considerable portion of their substance. The term protoplasm is now frequently so employed as to render it very desirable that its application should be restricted to a definite idea; but if we pay attention to the appearance and the most striking peculiarities of the protoplasmic masses described by Max Schultze § and by Kühne; ‖ and if also, as will be subsequently discussed, we consider that in their development the red blood corpuscles are formed at the expense of the cells composed of contractile protoplasm, in which metamorphosis the essential characters of the latter are lost, it is impossible to avoid expressing our opposition to the theory of Hensen. In fact, the forms which led Hensen to the above-mentioned view are susceptible of quite a different interpretation.

Brücke,¶ who observed such forms to be produced by the action of a two per cent. solution of boracic acid, considers that there is a porous structure composed of a non-contractile, very soft, colorless, perfectly transparent substance, which he further represents as the body of an animal, whose central part forms the nucleus of a nucleated corpuscle, and is free from hæmoglobin, whilst the remaining portion of the mass contains the whole of the hæmoglobin. Brücke considers that this latter portion accurately fills the inter-

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* Müller's *Archiv*, 1858, p. 178, Taf. viii.
† Virchow's *Archiv*, Band xxx., p. 417, Taf. xv., figs. 26 and 27.
‡ *Zeitschrift für wissenschaftliche Zoologie*, Band xi., p. 260, etc.
§ *Das Protoplasma der Rhizopoden und der Pflanzenzellen.* Leipzig, 1863.
‖ *Untersuchungen über das Protoplasma und die Contractilität.* Leipzig, 1864.
¶ *Wiener Berichte*, Band lvi., p. 79.

mediate spaces of the porous mass, and thus in combination with the parts free from pigment makes one continuous whole. To the colorless porous substance he has applied the term "*oekoid*," whilst he calls the contained substance the "*zooid*;" and he is of opinion that the retraction of the zooid either completely or partially from the oekoid explains the formation of the above-mentioned forms.

Stricker * agrees with Brücke in considering the oekoid to be the part enclosing the coloring matter, and as that which under certain conditions can retract towards the nucleus. He terms it the "body," at the same time attributing a greater amount of independence to the nucleus, and drawing attention to the analogy between the blood corpuscles of Amphibia and Mammals.

The question now arises, are the red blood corpuscles contractile as a whole, or is that part only contractile which is called the zooid by Brücke, or the body by Stricker?

Klebs † regarded the blood corpuscles of Mammals as contractile bodies, in consequence of his observations on the influence of temperature, though these have since been opposed by Max Schultze. The mulberry form he considered to correspond to the mobile condition, the curved-disk form to the quiescent condition, and the spherical form to the state of death. Rollett,‡ in consequence of his investigations upon the effects produced by electrical discharges on the blood corpuscles, is opposed to the view that they are contractile. He relies upon the facts that we always see the corpuscles in the interior of the vessels of the living animal in a state of merely passive movement; that blood corpuscles preserved outside the body for many months, or placed in blood destitute of oxygen but impregnated with carbonic acid, or in blood impregnated with carbonic oxide, behave themselves, when acted on by electrical shocks, in a manner essentially similar to those that have been recently taken from the living animal. Max Schultze § also, from his experiments on the influence of warmth on the non-nucleated corpuscles of Man and Mammals, arrived at the conclusion that these at least were not contractile; and Kühne ‖ expresses himself in similar terms.

We arrive here, however, at a point at which it appears necessary to determine what signification must be applied to the term contractility. Brücke, in the treatise above alluded to, justifying himself in speaking of the contraction of the zooid as of a living being, remarks that it would profit us nothing were we to refer the separation of the zooid from the oekoid, not to a contraction of the former, but to a process resembling coagulation, and that we have no guarantee that we have arrived nearer to the truth. A movement which we may designate by the term contraction certainly occurs; for the colored material unquestionably retreats from all sides towards the nucleus. What may be the causes of this contraction, and whether it may be compared in its essence with the contraction of a dying amœba, will probably long remain a subject of uncertainty; to the illumination of this darkness we may, however, soon attain.

Outline of the Chemistry of the Red Corpuscles.—The best-known constituent of the red blood corpuscles is hæmoglobin; this can easily be

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* Pflüger's *Archiv für Physiologie*, 1868, p. 591.

† *Centralblatt für die medicin. Wissenschaften*, 1863, p. 851.

‡ *Wiener Akad. Berichte*, Band l., pp. 190—200.

§ *Archiv für Mikroskop. Anatomie*, Band i., pp. 33, 34.

‖ *Physiolog. Chemie.* Leipzig, 1866, p. 191.

obtained in the crystalline condition. Hæmoglobin crystals have long been known as blood crystals, and have been subjected to microscopical scrutiny.

In the first instance they were recognized accidentally, Reichert* having observed them in a preparation from the guinea-pig preserved in alcohol, in the form of tetrahedra. Fünke,† Kunde,‡ Schwann,§ at a later period obtained the crystals methodically from blood treated with water, and found that the crystals of coloring matter from the blood of different animals presented different crystalline forms, whilst those from the same animal were for the most part identical. Those from different animals were at first considered to belong to very different crystalline systems.

It has been more recently ascertained that blood crystals can not only be obtained by destroying the blood corpuscles with water, but that an entire series of conditions which render the blood carmine in color by destruction of the corpuscles also lead to the production of hæmoglobin crystals. Thus, for instance, Rollett has shown that freezing and subsequent thawing of the blood, as well as the discharges of voltaic electricity; Rollett and A. Schmidt, that the alteration which the corpuscles undergo at the positive pole of a constant current; Max Schultze, that the elevation of the temperature of the blood by means of a water-bath at 60° C. (140° Fahr.); Bursy, that the addition of powdered salt; V. Wittich, that the addition of ether, or transmission of ether vapor; Böttcher, that the action of chloroform; and Kühne, that the alkaline salts of the biliary acids, produce the same effect.

From each drop of such lake-colored blood a large number of beautiful crystals may be obtained on the object slide of a microscope. Such crystals, obtained in constantly increasing numbers from different species of animals, and examined with still increasing care, are now proved to belong to two different crystalline systems. Lang‖ was the first to show that what were regarded as regular tetrahedra from the blood of the guinea-pig, when examined with a Nicol's prism in a polarizing microscope, appeared clear in four azimuths, and dark in four azimuths, and therefore that from their optical characters they belonged to the rhombic system: and further, that when compared with the prismatic crystals of human blood belonging to the same system, the following results were obtained. The lengths of the axes of the prisms of human blood present, according to measurements of the acute angle of the rhombic terminal plane (54° 1′), the proportion of 1 : 1,96 = 1 : 2·0,98; if then the second axis-length be divided by 2, the two axes would be of nearly equal length, which agrees well with the crystals from the blood of the guinea-pig.

The crystals of by far the greatest number of animals, however, occur either in the form of simple tetrahedra, or of tetrahedra with truncated angles and edges; or, like those of man, they form rhombic prisms, respecting which the recent treatise of Preyer ¶ may be consulted. The blood crystals of squirrels alone, formerly described as six-sided plates, appear, as shown by Von Lang,** to be six-sided plates belonging to the hexagonal system.

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* Müller's *Archiv*, *Jahrgang* 1849, p. 197.
† *Zeitschrift für rationelle Medicin*, N. F., Band i., p. 172; Band ii., p. 199.
‡ *Idem*, Band ii., p. 271.
§ *Handbuch der Physiol. Chemie*, Band i., p. 365; Band ii., p. 151.
‖ *Sitzungsberichte der Wiener Akademie*, Band xlvi., p. 85, *et seq.*
¶ Pflüger's *Archiv*, *Jahrgang* 1868, p. 365.
** *Loc. cit.*, p. 89.

Von Lang also first demonstrated that crystals of hæmoglobin, examined in two azimuths, with only one Nicol's prism over or under the object, exhibited colors different from those in the two intervening ones, and that they therefore present absorption phenomena in regard to light, in accordance with their crystalline form (Pleochroismus).

Besides hæmoglobin, a series of other substances have been ascribed to the blood corpuscles, constituting their colorless portion, which nevertheless appear to exist in very variable quantities in different animals. To these belong the albuminous bodies. The globulin, or paraglobulin of Kühne may be precipitated by means of carbonic acid from blood corpuscles modified to a certain degree by the action of water (Kühne, A. Schmidt, Stricker).

Moreover, an albuminous body, which still requires investigation, has been termed fibrinoid by Hoppe, and fibrin by Heynsius.

L. Hermann and Hoppe have demonstrated the presence of protagon, and Hoppe the presence of lecithin in the stroma of the blood corpuscles. As a consequence of the presence of hæmoglobin they contain a variable quantity of oxygen, and A. Schmidt has demonstrated the presence of carbonic acid in them. In addition to these substances there still occurs a certain proportion of salts differing qualitatively from the mineral matters of the plasma.

The Colorless Morphological Constituents of the Blood.—Amongst these the white corpuscles of the blood deserve to be first mentioned. These were distinguished by Hewson from the colored, and the great majority are characterized by the lively movements they are capable of performing.*

Max Schultze,† who has lately carefully investigated these forms, distinguishes several kinds in human blood. First, round cells, not attaining the size of the red blood corpuscles, composed of a thin layer of cell substance, investing one or two nuclei, which last are either spheroidal or flattened by mutual compression.

With these may be associated other forms, equalling in size the ordinary red blood corpuscles, and, like the former, possessing nuclei. Lastly, finely and coarsely granular amœboid cells are met with, and various intermediate forms between them.

In freshly drawn blood these last appear as more or less rounded or irregularly shaped forms. At a temperature of from 35° to 40° C. (95° to 104° Fahr.) lively movements, resembling the creeping motions of an amœba, occur. When the temperature, however, is raised above 40° C., the movements cease, and the cells harden.

As long as they are in active movement they are capable of absorbing small particles of coloring matter, as of carmine and anilin blue, and also milk globules, into the interior of their bodies. In reference to the further peculiarities of these true protoplasmic masses, I must refer to the first chapter of this manual. Besides the white corpuscles of the blood, Max Schultze admits, as constant constituents of human blood, irregularly formed masses of colorless globules, which he regards as fragments of cell substance.

There is a statement frequently met with in books, that, under certain circumstances, fat drops are met with in the blood, often in such quantity

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* Wharton Jones, *Philosophical Transactions*, 1846. Davaine, *Mémoire de la Société de Biologie*, 1850, Tom. ii., p. 103. Lieberkühn, Müller's *Archiv*, 1854, p. 11, *et seq.*

† *Archiv für Mikroskop. Anatomie*, Band i., p. 9.

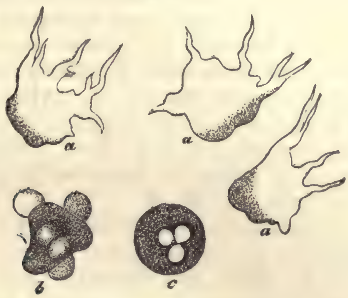
that the serum acquires a milky appearance, as in sucking animals,* and after the use of oleaginous food.† Oily matters, which have entered the blood, seem, however, to disappear with great rapidity. In the remarks made upon Schlemm's observations on kittens, Joh. Müller‡ states that he only found milky serum when the animal had shortly before ingested milk.

Yet another morphological constituent occurs in the so-called elementary corpuscles of Zimmerman.§ These have been held to be generators of the blood corpuscles. The greater number of them, obtained in the mode adopted by Zimmerman, from blood treated with salt, can be easily recognized as artificial products; that is to say, as the colorless remains of distorted red corpuscles (Hensen). It is not a matter of surprise that similar forms should also be frequently found in freshly prepared blood (Kneuttinger). Lastly, Max Schultze has demonstrated that the smallest elementary corpuscles of Zimmerman agree with his before-mentioned granules.

As regards the number of the white blood corpuscles, they are much less abundant in normal blood than in the red, and their relative number is subject to much greater variation. The variations depend upon the age, sex, period after food, and the vascular territory from which the blood examined has been taken.

Under all these different circumstances the number of the white blood corpuscles has been counted, according to the methods adopted for the enumeration of the red.‖

Fig. 94.



On the average there is, according to Welcker, one white corpuscle to 335 red, and according to Moleschott, one to 357.

Boys have one colorless to 226 colored. Men, one to 346. Old men, one to 381. Girls, one to 389. Young women who are menstruating, one to 247. The same women, when not menstruating, one to 405. Pregnant women, one to 281 (Moleschott).

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* Schlemm and Joh. Müller, Froriep's *Notizen*, Band xxv., 1829, p. 121.

† Kühne, *Physiolog. Chemie*, p. 181. Kölliker, *Gewebelehre*, 1867, p. 620.

‡ *Loc. cit.*

§ Rust's *Magazine*, Band lxvi., p. 171; Virchow's *Archiv*, Band xviii., p. 221; *Zeitschrift für wissenschaftliche Zoologie*, Band xi., p. 344. Hensen, *loc. cit.* p. 259. Max Schultze, *loc. cit.*, p. 39. Kneuttinger, *loc. cit.*, p. 5.

‖ Welcker, Präger, *Vierteljahrschrift*, *loc. cit.* Moleschott, *Wiener medicin. Wochenschrift*, 1854, No. 8. Hirt, *De Copia relativa Corpusculorum Sanguinis Alborum. Diss. inaug.* Lips., 1855. E. de Purg, Virchow's *Archiv*, Band viii., p. 301. Marfels. Moleschott's *Untersuchungen zur Naturlehre*, etc., Band i. p 61. Lorange, *Quomodo ratio Cellularum alb. et rub. mutetur*, etc., *Diss. inaug.* Regiomont, 1856.

Hirt found in the early morning, and in the fasting condition, that the proportion was one white corpuscle to 716 red; half an hour after breakfast, 1 : 347; two to three hours later, 1 : 1,154; ten minutes after a midday dinner, 1 : 1,592; half an hour after the same, 1 : 429; two to three hours after the same, 1 : 1,481; half an hour after tea, 1 : 544; two to three hours after tea, 1 : 1,227.

In the splenic vein, Hirt found the proportion to be 1 : 60; in the splenic artery, 1 : 2,260; in the hepatic vein, 1 : 170; and in the portal vein, 1 : 740.

Several kinds of colorless morphological constituents can likewise be distinguished in the blood of the Frog * (fig. 94, *a*); namely, the ordinary amœboid cells, and the so-called granule cells, filled with highly refractile granules. The former (fig. 94) exhibit more, the latter less lively changes of form, associated in freshly drawn blood with locomotive movements, and likewise take up into their interior milk globules and particles of coloring matter. † Preyer ‡ saw portions of the red blood corpuscles of extravasated blood in Amphibia taken up by white blood corpuscles, and thus explained the nature and mode of occurrence of the bodies that were previously called blood-corpuscle-holding cells. When acted upon by induced currents, and the discharges of voltaic electricity, these cells become round, § just as occurs, according to Kühne, in amœbæ when irritated. Golubew showed that the cells of the frog, after having been made to contract by the application of a stimulus, recommence their movements. The character of these movements, however, is no longer the same as before the irritation; for, whilst the processes are in the first instance conical and finely pointed, on the recommencement of the movement after excitation they are more rounded, as well as shorter and broader, are quickly protruded, and are again withdrawn, to reappear in the immediate proximity; so that a kind of undulation runs round the corpuscle (fig. 94, *b*). After a short time, either the original character of the movement reappears, or the corpuscles expand on the recurrence of movements, into a flat disk. When in either of these phases, increased strength of excitation immediately causes the corpuscle to reassume the spheroidal form (fig. 94, *c*).

After the continuous application of strong shocks the white corpuscles become destroyed, molecular movements occur in the swollen cells, or they are ultimately reduced to disks, and discharge their granules. A great number of these cells can be observed in an isolated condition if a drop of blood, recently obtained from a Newt or Frog, be brought upon a glass cover placed over a moist cell, and the drop, whilst freely dependent, allowed to coagulate. It is soon observable, when the zone of serum extends beyond the limits of the clot, that in this zone, in consequence of an active migration from the coagulum, numerous amœboid cells are present, and that they have accumulated on the surface of the coagulum.

Sclarewsky ‖ has discussed this phenomenon of the migration of the white blood corpuscles from the coagulum at considerable length, as it may be observed in blood coagulated in capillary tubes. The above-mentioned simple experiment is far better adapted for the isolation of the cells for microscopi-

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* Rindfleisch, *loc. cit.*, p. 21. Kneuttinger, *loc. cit.*, p. 10, *et seq.* Golubew, *Sitzungsberichte der Wiener Akademie*, Band lvii., p. 555.

† Recklinghausen, Virchow's *Archiv*, Band xxviii., p. 185; *Die Lymphgefässe und ihre Beziehung zum Bindegewebe.* Berlin, 1862, p. 22.

‡ *Loc. cit.*, p. 423.

§ Neumann, Reichert and Du Bois' *Archiv*, 1867, p. 31. Golubew, *loc. cit.*, p. 555

‖ Pflüger's *Archiv*, 1868, p. 660.

cal observation, and the investigations which can thus be made into the details of the migration of the individual cells render it clear that the individual movement of the cells is the chief, if not the exclusive, cause of their emigration. The causes which must be admitted for the movements leading to this migration are still to be ascertained.

Besides these migrating cells a few small colorless structures, presenting the appearance of free nuclei, occur in the blood of the Frog at all periods of the year; lastly, we meet, in the blood of the frog, with the fusiform cells, first exactly described by Von Recklinghausen,* which, however, vary in number with the period of the year, being especially abundant in spring. They possess a bright homogeneous cell substance, and a granular oval nucleus.

Von Recklinghausen, who has acquainted us with the remarkable fact that if the freshly drawn blood of the Frog be preserved in moist air, after a short time an active process of cell formation takes place in it, which ultimately leads to the formation of red blood corpuscles, has also furnished some description of the intermediate forms that may be observed. Sclarewsky† and Golubew‡ have also been lately occupied with the investigation of the intermediate forms between the white and red blood corpuscles. From the statement of these authors it is to be concluded that the pale cells, which otherwise resemble red blood corpuscles, occurring in the blood of the Frog, and described by earlier observers, are to be regarded as amongst these intermediate forms.§

From the facts just mentioned, we are directly conducted to the difficult questions of the origin and regeneration of the organized constituents of the blood.

Development of the Blood Corpuscles.

The first colored blood corpuscles in the fowl originate contemporaneously with the formation of the first vessels in the germinal area,‖ or in the vascular area and *area opaca*,¶ and they either detach themselves from the walls of the vascular spaces (Afanasieff), hanging together in isolated groups (blood islands, Wolf and Pander), or they may originate, according to the view of His, in the form of groups, from large masses of protoplasm in the walls of the vessels, and at a later period burst into their lumen. Soon after the coalescence of the vessels with the heart, these primordial blood corpuscles, which are lying ready to be borne onwards by the current, are floated off, either separately or in groups (His). The primordial blood cells exhibit numerous processes and outgrowths (His). Moreover, the colored blood corpuscles circulating during the later periods of intra-oval life exhibit numerous forms attributable to fission, which have been described and depicted by Remak.**

In the tail of young tadpoles the newly formed vessels are found to be filled with peculiar, short, compressed, fusiform bodies, flattened on two of

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* Max Schultze's *Archiv*, Band ii., p. 137.

† *Centralblatt für die medicin. Wissenschaften*, 1867, p. 865.

‡ *Loc. cit.*, p. 566.

§ Wharton Jones, *Philosophical Transactions*, 1846. Hensen, *loc. cit.*, p. 263.

‖ Afanasieff, *Sitzungsberichte der Wiener Akademie*, Band liii., p. 560.

¶ His, *Untersuchungen über die erste Anlage des Wirbelthierleibes.* Leipzig, 1868, p. 95.

** *Untersuchungen über die Entwickelung der Wirbelthiere.* Berlin, 1855, p. 164: Müller's *Archiv*, 1858 p. 178.

their sides, which present a very light yellow tint, and contain numerous yolk granules, but are otherwise homogeneous.

In addition to these primary cells there appear, it would seem, concomitantly with the progressive development of the intestinal tract, a constantly increasing number of white corpuscles. The number of the cells filled with yolk granules, on the other hand, gradually diminishes. We soon after meet with the intermediate forms already described as existing in adult animals, together with colored blood corpuscles of the form ordinarily present in the blood of the Frog.

In Mammals there may be observed in the blood of the embryo, at an early stage, nucleated colored blood corpuscles in process of fission. At a later period these forms are less abundant, in accordance with the progressive development of the embryo and of the spleen in particular (Kölliker), and we meet with numerous white corpuscles in the blood of the liver, which become metamorphosed into colored nucleated blood corpuscles. Up to a certain period of embryonic life only nucleated red blood corpuscles are present in the blood (Kölliker). The non-nucleated first appear at a later period, their relative number then undergoing a constant increase. According to Kölliker, non-nucleated corpuscles are not present in the blood of fœtal sheep measuring three and a half inches in length; in those of nine inches long they are but seldom found, whilst they constitute the majority in fœtuses that are thirteen inches in length.* According to Robin,† in human embryos measuring thirty millimetres, about one-half of the total number of blood corpuscles are destitute of nuclei; a few nucleated corpuscles are still discoverable in embryos of the fourth month, and even at still later periods.

As has already been mentioned, the red blood corpuscles can be regenerated in large numbers in the blood of adult animals, and this is accomplished at the expense of the white corpuscles, as was demonstrated in the case of the frog by V. Recklinghausen, and still more recently again by Golubew. Fission of the red blood corpuscles in adult animals has only been observed in a few rare instances.

Whether the colorless corpuscles always undergo multiplication within the blood itself, and by what mode of cell genesis they multiply, are still open questions. It is certain that a large number of white corpuscles are added to the blood, not only during the period of development and of growth of the animal organism, but also throughout life, by the agency of the lymph current, the corpuscles of this current originating in localized germ-producing organs, situated external to the blood (lymphatic glands).

If the continual addition of such young cells had only as an object the supply of material for the regeneration of the red blood corpuscles, it would demonstrate that the latter are very unstable structures in which rapid metamorphoses take place. Independently, however, of the circumstance that it is possible the white corpuscles themselves undergo disintegration in the blood, we know as a fact that they migrate from the interior of the vessels into the tissues, and that they participate in effecting certain plastic processes in these tissues; on the other hand, up to the present time we are acquainted with only two regularly recurring processes, in one of which —menstruation—there certainly occurs, whilst in the other—the prepara-

* Kölliker, *Zeitschrift für rationelle Medicin*, Band iv., p. 112; *Gewebelehre.* Leipzig, 1867, p. 637. E. H. Weber and Kölliker, *Zeitschrift für rationelle Medicin*, Band iv., p. 160.

† *Journal de la Physiologie.* Paris, 1858, p. 288.

tion of bile*—there very probably occurs the destruction of a large number of red blood corpuscles.

Moreover, the observations on the disintegration of the red blood corpuscles may here be alluded to, that have been described as taking place in the formation of pigment in the spleen, in the blood-corpuscle-holding cells of the spleen (*vide* spleen), and of the medulla of the bones; but in regard to the period of the occurrence of which during life nothing is at present known.

Forms that may be supposed to be transitional between the white and the red corpuscles contained in the general mass of the blood of Mammals have however been described by Erb† under the term of "granular blood corpuscles," appearing in particular after artificial losses of blood.

Kölliker‡ adverts to the fact that he long ago found similar forms in the blood of the young sucking mouse. The mode in which they originate from the nucleated white corpuscles, and the stages of their conversion into the ordinary form of the red blood corpuscles, still require to be systematically followed out. In the blood of leucæmic patients nucleated red blood corpuscles are frequently to be found presenting the appearance of the nucleated embryonic blood corpuscles of Mammals and of Man.

Reference may here also be made to the statements advanced respecting the presence of red corpuscles in process of development in the pulp of the spleen. (See the chapter on the Spleen.)

In the last place, attention has very recently been directed by Neumann§ to the nucleated red corpuscles constantly present in the medulla, and especially in the red medulla of bones (Man, Rabbit); and Bizzozero‖ has corroborated the observations of Neumann in the case of Man, the Rabbit, and the Mouse. Both inquirers describe a complete series of transitional forms existing between the white nucleated and the non-nucleated red blood corpuscles, and associate the marrow of the bones consequently with the development of the blood. Still further communications on this function of the bony marrow have just been made by Hoyer.¶

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* Kühne, *Physiologische Chemie*, p. 88.
† Virchow's *Archiv*, Band xxxiv., p. 138, Taf. iv.
‡ *Gewebelehre.*
§ *Centralblatt für die medicin. Wissenschaft.*, *Jahr.* 1868, p. 689; and *Archiv für Heilkunde*, 1869, p. 640.
‖ *Centralblatt*, 1868, p. 881; and 1869, p. 149.
¶ *Centralblatt*, 1869, pp. 244 and 257.

CHAPTER XIV.

THE SALIVARY GLANDS.

By E. F. W. PFLÜGER.

§ 1. General Plan of Structure.—The salivary glands represented by the parotid, submaxillary, and sublingual glands, when examined with the naked eye, appear to be rounded or polygonal yellowish-white masses flattened by mutual pressure, and opening by hollow peduncles into a common excretory duct. The gland, in each instance, consists of a tube branching frequently in a tree-like manner, and lined throughout by a layer of epithelial cells. The numerous terminal branches, named alveoli, are lined by large tesselated epithelium, whilst the other portions are invested either with columnar or small tesselated epithelium, and present a clavate form, being arranged like grapes on the principal excretory duct. The salivary glands consequently belong to the group of acinous glands. The alveoli, however, with their secondary and tertiary processes, must not always be regarded as possessing the form of a berry, since they not seldom appear to be quite cylindrical, or only slightly contracted, where they spring from the trunk. The number of alveoli belonging to one of the smallest excretory ducts is so large that they lie tightly compressed and flattened in a polygonal manner against one another, leaving only a very small space for interstitial tissue.

§ 2. The Alveoli.—If a section of the tubes measuring 0·030 millimetre in diameter be made, a canal and a wall may be distinguished. Even in glands hardened in alcohol it may easily be perceived that in the somewhat larger alveoli the cavity is of very variable calibre, and may attain the mean diameter of a salivary cell, but may be also both extraordinarily fine (1—2 μ) and several in number in one and the same alveolus. The central canal gives off, as I have found, in conjunction with Mr. Anton Ewald, student in medicine, extremely fine tubuli (salivary capillaries), which penetrate between the salivary cells and also between the tunica propria and the epithelial cells; so that these, like the cells of the liver, are surrounded by tubuli that can be injected with Prussian blue, and appear to proceed from one alveolus to another. The parietes of the tubes, composed in general of a single layer of cells, are invested externally by an extremely fine, and when fresh, completely structureless membrane, called the membrana propria. The existence of this may be demonstrated by macerating the fresh submaxillary gland with distilled water, when the membrane becomes raised from the epithelium, often to a considerable distance, in the form of a hyaline vesicle. Recently the presence of a membrana propria in glands generally has been called into question, and especially by Schlüter,* in the case of the salivary glands. In order to exhibit it I would recommend the pancreas of the rabbit to lie for four days in iodized serum of a light sherry color, and subsequently for two days in five cubic centimetres of diluted chromic acid,

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* *Disquisit. Mic. et Phys. de Gland. Salivar. Vratisl*, 1865; *Inaug. Diss.*

containing one-fiftieth per cent. By an action that is clearly of a digestive nature, the epithelial cells are in part detached, and obviously lie in a wide hyaline sac which they by no means fill. This appearance will incontestably demonstrate the existence of a membrana propria, forming a closed and continuous membrane.

A question of a totally different nature is whether this membrane may be regarded as being composed of flat cells fused or coalesced together. According to Boll * and Kölliker, it is composed of anastomosing connective-tissue cells that form a reticulum in which the alveolus lies as in a cavity of trellis or wicker-work. However plausible this view may appear on *à priori* grounds, there are facts which can scarcely be brought into unison with it. Thus, (1) on examination of the membrana propria in fresh preparations, I have never been able to distinguish a nucleus, although I tested for it with dilute chromic acid which causes the nuclei of the epithelial cells to come into prominent relief, and although the quadripolar flattened cells regarded by Boll and Kölliker as constituents of the membrana propria frequently contain a very brilliant large nucleus, which, according to Boll, may be round and very thick. (2) The vesicular elevation of the membrana propria from the salivary cells, consequent upon diffusion, presupposes a continuous membrane, which in fact comes into view, whilst it is impossible to see any reticulum. (3) The small quadripolar cells of the reticulum so rarely occur in rabbits that they are by no means sufficient to furnish an investment to all the alveoli. (4) The quadripolar cells are unquestionably connected with the epithelial cells by means of processes, and cannot consequently be regarded as connective tissue cells, a point into the consideration of which it will be hereafter necessary to enter. The view entertained by Boll and Kölliker has not, consequently, at present received adequate confirmation.

In the next place, as regards the contents of the alveoli. These consist of cells filled with numerous granules, so that the gland substance appears black by transmitted light, rendering it impossible to distinguish either the cell contour lines or the nuclei. Such are the appearances presented by perfectly fresh preparations made from the gland whilst still warm and almost living, if moistened with the aqueous humor. In diluted chromic acid, containing one-fiftieth per cent., the greater part of the granules quickly dissolve, whilst the alveolus becomes transparent, and presents the most beautiful mosaic of cells. For this experiment the submaxillary glands of the rabbit are admirably adapted. Every cell is rendered polygonal by mutual compression, and presents sharply defined bright double contours. For the most part they only form a single layer, which lines the central canal of the gland, and is differentiated from this by a sharp contour line. In most animals the membrana propria is easily elevated. The cells adhere very strongly to one another, so that after being detached from the membrana propria they still hang together in small groups. It is noteworthy in regard to the size of the epithelial cells, that as a general rule those contained in the same alveolus are of nearly the same size. But if we compare those belonging to different alveoli, they are found to be of very different dimensions. It is possible that the small epithelial cells may belong to alveoli of smaller diameter. There may, however, be found all the transitional forms between the two, so that we are here dealing only

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* Franz Boll, *Ueber den Bau der Thränendrüse im Archiv f. Mikroskop. Anatomie*, Band iv., 1868, p. 146.

with the same gland substance in different stages of development. This remark applies also to adult animals.

If we now proceed to examine with more minuteness the salivary cells of the alveoli, I must in the first place observe that they appear to be invested by a membrane both towards the lumen of the tube and where they are in apposition with each other. It is important to observe that the double contours of two salivary cells in contact with one another are not always perfectly distinct, as though at some points there existed a still more intimate union between them. The protoplasm of the salivary cells is tenacious, finely granular, and frequently striated. A cell of this kind may give rise to the impression that its protoplasm is composed of innumerable extremely fine fibrils. The average size of the salivary cells is 0·014 millimetre in diameter. The largest epithelia of this kind with which I am acquainted I have found in certain alveoli of the salivary glands of the Ox.

An extremely pale spherical nucleus is to be found in the interior of the protoplasm in all fresh specimens, and even in those that have been moistened with diluted acids. After the action of the acid has been long continued, it becomes highly refractile, and presents a dark and sometimes double contour line. It then gradually shrinks, and applies itself as a flat disk to the wall of the cell, which frequently renders its recognition a matter of difficulty. The cell nucleus lies eccentrically to the salivary cell and alveolus, and immediately beneath the membrana propria. Its average size in the fresh condition, after being brought into view by dilute acids, amounts

Fig. 95.

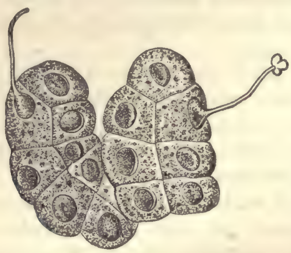

Fig. 95. Isolated alveoli of the Rabbit, exhibiting processes. Magnified 480 diameters.

to 0·306 millimetre. The most remarkable peculiarity presented by the nuclei of the cells, when fresh, is that they give off an extremely delicate fibre (fig. 95), which often penetrates that surface of the salivary cell which is in contact with the membrana propria. I have seen these caudate nuclei in perfectly fresh specimens. The submaxillary gland of the rabbit or pig is best adapted for their demonstration. The existence of the processes of the nculei has been corroborated by C. Otto Weber, as well as by Boll, whilst by Kölliker and Heidenhain, though undoubtedly incorrectly, it is denied. The latter,* it is remarkable, has himself drawn a thick process, attached with such remarkable distinctness to the nucleus of an isolated salivary cell, receiving as it leaves this a sheath of the cell membrane, that, upon the ground of this positive observation alone, I should draw the con-

* R. Heidenhain, *Studien des physiologischen Instituts zu Breslau*, 1858, Taf. iv., fig. 13 *x*.

clusion that the process is frequently not seen in connection with the cell, because it is destroyed in putting up the preparation. The nuclear process appears to be hollow, since it often discharges a large quantity of tenacious material, which clearly proceeds from the nucleus. In consequence of the nuclear process leaving the cell, it gives the latter the appearance of being stalked, as has been seen by Schlüter, myself, Gianuzzi, Boll, and Kölliker. According to the descriptions given by Schlüter and myself, the cell processes are often of great length, branch, coalesce (Schlüter), and support the alveolar cells like berries.

There is never more than one nucleus in each salivary cell. Occasionally, indeed, there appear to be more, but in such cases there is always a doubt whether the line of division between two adjoining cells is perceptible.

According to Heidenhain, there are two kinds of salivary cells, of which one contains mucus, but no albumen; the other albumen, but no mucus. The former he denominates "mucous-cells," the latter "albuminous-cells." Both are glassy, transparent, and delicately striated; the latter are, in addition, finely granular. Where mucous cells predominate, as in the submaxillary gland of the dog, cat, ox, and sheep, they may perhaps represent the young condition of the albuminous cells. In the rabbit, at least in the submaxillary gland,* no mucous cells are, according to this observer, to be found.

Besides the points already described, there still remains to be noticed a structure, first mentioned by Gianuzzi, and to which he has applied the term semi-lunar body.†

When sections are made of hardened salivary glands, there appears here and there a concavo-convex lenticular lamina, usually of very small thickness, which adheres intimately to the alveolus surrounding the salivary cells that lie in its cavity, and presents, on section, a semi-lunar form. But inasmuch as, on investigation of fresh glands, I was never able to see the semi-lunar body, and found that even in rabbits it eluded my observation, I was inclined, since this structure is only demonstrable in those animals which have mucous cells, to regard the semi-lunar body as an artificial product, and as originating in the *post-mortem* formation of a mucous vesicle, compressing the cell protoplasm towards the wall. And it is remarkable that, according to the recent investigations of Heidenhain, the submaxillary gland of the dog, when the mucus is withdrawn from it, no longer presents the demi-lune, but resembles the same gland in the rabbit.‡ The elimination of the mucus is effected by exciting the gland to react through the nerves for many hours, whereby the mucus and the mucus-forming materials are consumed.

Later inquirers do not agree with me in my opinion regarding the demi-lune; nevertheless they completely justify it, by each one giving a different interpretation of its nature. C. Ludwig and Gianuzzi ascribed to it a laminated structure, and described the blackening it underwent from the action of perosmic acid, and the reddening with carmine. They were unable to see nuclei distinctly. Boll and Kölliker described the "half-moon" as composed of connective tissue, which, firmly adherent to the alveolus, represents the cells constituting the reticulum already referred to. Heidenhain main-

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* See Heidenhain, *loc. cit.*, p. 6.

† S. Gianuzzi, "On the effects of acceleration of the blood currents on the secretion of Saliva;" *Ber. d. K. Sächs. Ges. d. wiss. Math. Phys. Classe, Sitzung vom* Nov. 27, 1865.

‡ Heidenhain, *loc. cit.*, Taf. ii., fig. 5.

tained that the demi-lune was formed by a layer of young epithelial cells, destined to supply the place of those salivary cells which were undergoing disintegration. I believe this view to be not an unreasonable one, for inasmuch as in the submaxillary gland of the dog the protoplasm of the mucous cells is scarcely, if at all, tinted with solutions of carmine, whilst the small nuclei lying at the periphery, as well as the numerous superimposed long cell processes running outward, are deeply stained, we have a sufficient explanation of the occurrence of a complete marginal zone in the alveolus. But since the term "demi-lune" can possess such different significations, it is better to avoid its use entirely.

§ 3. THE EXCRETORY DUCTS.—In the interior of the gland, besides the structures already described, are tubes often of considerable size, and lined with cylindrical epithelium, to which the name of excretory ducts is applied. Close investigation shows that they must possess great functional importance. As evidence of this, I would first remark that if a dog be killed as rapidly as possible, and fine sections be prepared from the submaxillary gland, transparent drops may be seen exuding from the columnar cells lining the excretory ducts, and some of these, having already become detached, lie in the lumen of the tube, appearing in the form of round, sharply defined, clear spherules. These unquestionably proceed from the cylindrical epithelium.

Fig. 96.

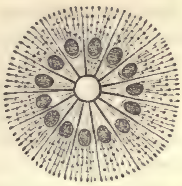

Fig. 96. Transverse section of a fresh salivary tube in diluted chromic acid of one-fiftieth per cent. Magnified 480 diameters.

But inasmuch as drops, presenting precisely the same appearances, are found in freshly secreted saliva, that has been caused to flow by irritation of the gland, it would appear highly probable that these cylindrical epithelial cells also belong to the secretory apparatus. Anatomical examination tells still more strongly in favor of the importance of these structures, since it then appears that the thickness of the wall of the duct, as we advance towards its peripherical distribution, instead of, as might be expected, diminishing, undergoes material increase. The thickening of the wall is in general occasioned by the elongation of the cylindrical cells, which, however, never form more than a single layer. Besides this, the wider ducts exhibit more or less strongly marked outgrowths, lined with the same epithelium. If the ramifications of the ducts be traced in a peripherical direction, fine passages are at length met with, having a diameter of 0·010 millimetre, possessing the same epithelial lining as the larger ones, and, if I am not mistaken, terminating in blind extremities; these are the secretory tubules—that is, the capillaries of the salivary ducts, having the same tenuity as the biliary capillaries, and leading to the alveoli. In a word, these excretory ducts, or *salivary tubes*, possess diverticula of various form. Not unfrequently they form loops or bend suddenly.

If we now proceed to the study of the characters of the columnar epithelium, the cells will be found to possess an average diameter of 0·004 millimetre, and to be of very variable length. The cylindrical epithelial cells are so well defined at their points of contact with each other, and on their free surfaces directed towards the interior of the tube, that they appear to possess a membranous wall; and these walls, towards the lumen of the tube, are united into a highly refractile continuous layer, the cells being here intimately adherent. They are, however, strongly adherent elsewhere, to so great an extent, indeed, that when in the fresh condition it is impossible to isolate them. If the surface of the tube be examined, a beautiful mosaic of cells comes into view, the transverse section of the cells being for the most part completely filled by a well-defined nucleus. The cell contents, when a freshly made transverse section of the salivary duct of a dog is examined, appears to be perfectly hyaline. This animal is well adapted for the purpose, because the toughness of the gland (submaxillary) permits fine sections to be made of it whilst still warm, after removal from the body. The most remarkable feature of these cylindrical epithelial cells is presented by the surface turned from the canal, and which is immediately in contact with the membrana propria. From this spring a large number of extremely fine varicose hairs, quite a bunch or pencil of such hairs proceeding from each cell. The surface of the tube composed of these cylindrical cells, always easily capable of detachment from the membrana propria, appears, on account of the equality in length of the several hairs, like a thick brush. These extraordinarily fine fibrils may be observed in any of the fluids in which the fresh gland can be properly examined. There may also be constantly seen, on focussing the surface of the salivary duct, fine points, which represent the optic transverse section of these varicose fibrils. For these reasons I am not disposed to regard these brushes as artificial products, which have originated by a splitting of the peripheric portion of the cells.

Whilst in most cells the fibres commence immediately below the nucleus, it may be observed in some preparations, in which the cells have been isolated in iodized serum, that a few fibrils take origin from a higher point in the interior of the cell. In many of these cylinders the body of the cell very constantly presents the appearance of being delicately transversely striated. In the greater number of instances, however, that portion of the cell which is next to the canal remains transparent. From preparations made with iodized serum, it can be shown that some of these cylindrical cells, in consequence of the smallness or disappearance of their processes, and the assumption of a polygonal form, approximate closely to the flattened epithelium found in the alveoli. This similarity also extends to the cell contents and to the nucleus.

Besides these extremely fine processes of the columnar cylinder cells, resembling the fibrils proceeding from the axis cylinder of a nerve, others of greater thickness, and of high refractive power, may be observed to be given off from their sides. The significance of all these processes will be hereafter discussed at greater length.

Lastly, as regards the dimensions of the calibre of the tubes, it is found that they vary from a diameter of 0·030 millimetre or less to a size easily recognizable with the naked eye. The enlargement is essentially effected by increased diameter of the lumen, and to a less extent by increased length of the columnar epithelium. I have met with such canals in the interior of the glands of the dog, the lumen of which had a diameter of 0·1 millimetre or more.

Besides the salivary tubes, other tubes are found in the salivary glands,

varying considerably in diameter, and lined by a small description of tesselated epithelium, that generally diminishes with the bore of the tube. These may be injected through the ordinary excretory ducts, as well as through the salivary tubes, and ultimately form by their ramifications passages which have only a diameter of 0·007 millimetre or less, and are lined by a very small-celled pavement epithelium. These passages constitute without doubt excretory ducts proceeding from the alveoli, and form a stage in that developmental metamorphosis of the gland which exists even in the adult.

Whether the salivary tubes, which are continuous with these excretory ducts lined by pavement epithelium, communicate with the alveoli, and in what way this communication, if present, is effected, demands further investigation. I know for a fact that a mosiac of salivary cells may lie in immediate juxtaposition to columnar epithelium; but it is very rare for the canal of a salivary tube to be directly continuous with a canal which is lined with salivary cells. I am of opinion that the communication between the salivary tubes and the alveoli is effected by means of very fine passages (salivary capillaries). The proper excretory ducts (Ductus Whartonianus, Stenonianus, etc.) are generally admitted to be lined by an epithelium, consisting of a single layer of short cylindrical cells. Boll, however, describes the epithelium as composed of tesselated cells. The wall is strengthened by fibres of connective tissue, with numerous elastic fibres and membranes, as well as by smooth muscular fibre cells.

§ 4. Distribution of Nerves in the Salivary Gland.—The nerve tissue of the salivary glands consists of ganglion cells and fibres. The latter are composed both of medullated, which constitute the greater number, and of pale nerves.

Three different kinds of pale nerves may be distinguished.

a. Fasciculi of extremely delicate transparent fibres, presenting the characters of axis cylinders, and invested with a sheath of connective tissue, containing nuclei. Were it requisite to adduce any proofs of the nervous nature of these fasciculi, it might be pointed out that these pale fibres form from time to time large fusiform varicosities, consisting of nerve medulla, characterized by its double dark contour. The pale fibre between two such varicosities differs in no respect from that lying in their immediate proximity. The above feature, however, renders it probable that these pale fibres conceal a thin layer of nerve medulla between the axis cylinder and the sheath. At the same time, neither a special investing sheath nor nuclei can be demonstrated around the individual primitive fibres, as indeed follows from what has been above stated, and these consequently, in the fresh condition, possess the appearance of naked axis cylinders.

b. A second kind of pale nerve fibre found in the salivary glands I shall denominate gelatinous fibres. They consist apparently of bands of finely granular protoplasm, lying in a sheath of connective tissue, in which are nuclei, and presenting exactly the same appearance and behavior as the protoplasm of the large ganglionic cells of the glands. Such gelatinous fibres may be observed to leave the ganglion cells, and hence are unquestionably of a nervous nature. They are probably composed of fasciculi of extremely fine varicose fibrillæ, which, lying in close apposition, give the impression of a finely granular, somewhat striated protoplasm. These fibres present the same appearance as the so-called protoplasmic processes of the nerve cells of the cerebro-spinal organs.

c. A third kind of pale fibre is composed of bundles of somewhat tougher, more highly refractile, very fine (0·0005 millimetre) fibrils, which likewise

lie in a tube of connective tissue containing oval nuclei. These are liable to all the objections that have been raised on various sides against the nervous nature of the fibres of Remak.

The medullated fibres, which are present in extraordinary numbers in all parts of the salivary glands, and of all sizes down to those of only 0·0015 millimetre in diameter, present a series of very remarkable peculiarities. In the first place they have such delicate and pliable sheaths, that they sometimes appear to be destitute of them. In accordance with this, varicosities form in the coarser trunks, as in the fibres of the brain or spinal cord (see Fig. 97), where, however, they become still larger, and form more easily than amongst these. On account of the extraordinary delicacy of the sheath these fibres tear with remarkable facility, and pour forth their contents in the form of myelin drops, which rapidly become stained of a blue-black color by osmic acid, like these nerves themselves.

Fig. 97.

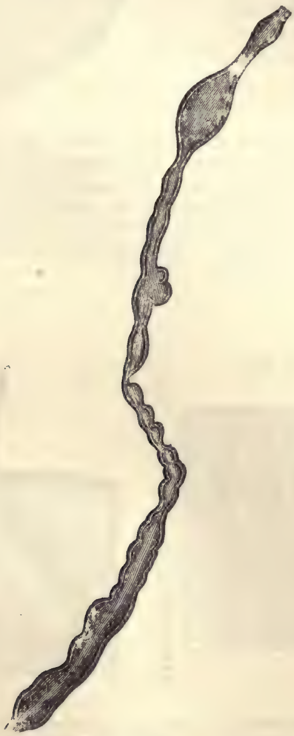

Fig. 97. The preparation was taken from the submaxillary gland of the Ox, and was blackened with perosmic acid. Magnified 590 diameters.

A second peculiarity of the medullated glandular nerves is exhibited in their mode of division, the division occurring so frequently as to have been seen by almost all observers. According to my own observation, the number of divisions increases in a most unusual manner towards the periphery,

so that almost feathery medullated primitive fibres lie between the alveoli, and give off branches in all directions.

Fig. 98.

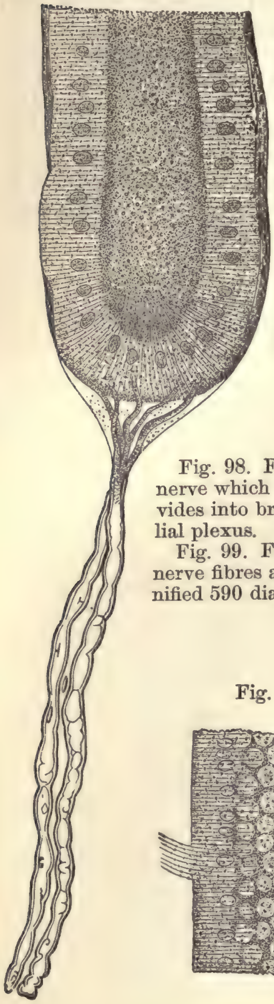

Fig. 99.

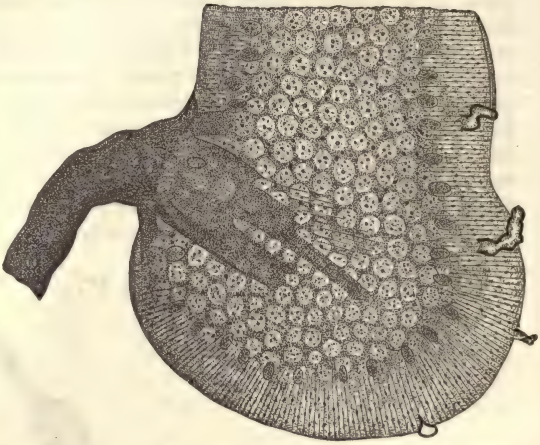

Fig. 98. Fresh specimen. From the Ox, exhibiting a medullated nerve which penetrates the membrana propria. The axis cylinder divides into branches upon the membrana propria to form the sub-epithelial plexus. Magnified 590 diameters.

Fig. 99. From the Ox, showing the termination of one of the thickest nerve fibres at a thick salivary tube blackened by perosmic acid. Magnified 590 diameters.

Fig. 100.

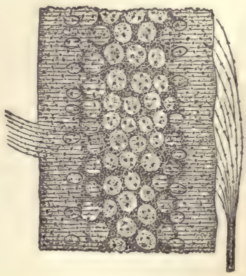

Fig. 101.

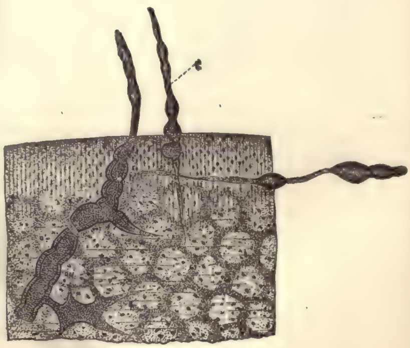

Fig. 100. Showing an axis cylinder breaking up into fibrils which are continuous with the fibrils of the columnar epithelium. Magnified 590 diameters.

Fig. 101. From the Ox, showing medullated and in part varicose nerves blackened by perosmic acid, which branch in the sub-epithelial plexus, and one of which (n) can be distinctly traced into the processes of the columnar epithelial cells. The preparation exhibits a marginal portion of the surface of a salivary tube. Magnified 800 diameters.

If we now proceed to the consideration of the terminal organs of the nerve fibres, we must first discuss the relations these bear to the proper tissue of

the gland. The salivary tubes, with which we shall best commence our description, are accompanied by numerous bands of medullated nerve fibres of very various size. Many are in the most intimate relation with the tubes, as is shown in the accompanying figures. In one instance the specimen was fresh (fig. 98), in another it was stained by maceration in perosmic acid (fig. 99).

These nerves, as seen in figs. 98 and 99, perforate the membrana propria, and then break up into a number of fibres, which become finer by further subdivision, and wind around the outside of the columnar epithelial cells, to form a sub-epithelial plexus, which demands still closer examination. The fibrils lying on the membrana propria are pale and soft, and give the impression of naked axis cylinders. But that they are accompanied for some distance by the nerve medulla is recognized by the blackening of the osmic acid preparations around the termination of the thicker primitive fibres. The axis cylinders running on the membrana propria branch ultimately into the finest possible varicose fibrils, which have precisely the same characters as the fibrils which emerge and join them from the columnar epithelial cells. It is frequently observable that the last ramifications of the axis cylinder are continuous with these fibrils; and that the columnar cells thus represent the continuations of the finer and the finest medullated nerves with the sub-epithelial plexus is frequently capable of direct proof, as appears from an examination of fig. 100. We may even succeed, though rarely (fig. 102), in effecting the complete isolation of all parts, and in thus showing the continuity of the medullated nerves with the processes of the columnar cells. It may thus be rendered evident that these fine processes are in direct continuity with the axis cylinder, from which they do not in any respect differ.

Fig. 102.

Fig. 102. From the Rabbit, exhibiting a medullated nerve, becoming continuous with an axis cylinder which passes directly into the process of a cylinder cell, and directly opens into the columnar cell. Magnified 590 diameters.

At the same time it may be remarked that the axis cylinder of the afferent nerves appears to be thicker than the fibrillar processes of the columnar

cells, which must consequently be regarded as continuations of the fibrillæ of the axis cylinder. After the nerve has penetrated the membrana propria of the salivary tube, the axis cylinder either immediately terminates, or does so after it has first run for some distance upon the membrana propria; in the latter case it runs between this and the fibrillar processes of the columnar epithelial cells.

When we consider the incredibly large supply of nervous fibrils that lies beneath the membrana propria, the question of the object of this abundance naturally suggests itself. After studying with greater exactitude the laws of the growth of glandular epithelium, we shall find that a completely satisfactory solution of this question may be attained. I shall treat of this point, however, at a later period. I would only mention here that numerous young salivary cells develop from every columnar cell with its fibrillar processes, and that each of these must again have its proper nerves. This is true also in the case of the adult animal. From the almost imperceptibly fine fibrils of the columnar cells the fibres of the epithelium cells of the alveoli proceed, which we shall now subject to a careful consideration.

Two kinds of nerve termination are to be distinguished in the alveoli:—

I. The most important is that of the medullated primitive fibres. These

Fig. 103.

Fig. 103. From the Ox. An alveolus with the terminations of medullated nerves which have been blackened by perosmic acid. Magnified 590 diameters.

branch very frequently between the alveoli, apply themselves to the membrana propria, and usually give off at the point where they penetrate it several branches, which run for some distance on its outer surface to the nearest epithelial cells, in order to penetrate over these into the alveolus (fig. 103). The nerve becomes blackened by perosmic acid up to the point where it perforates the membrana propria; at this point the medulla appears to cease (figs. 104 and 107). That the membrana propria is perforated is shown in the most striking manner by the circumstance that the continuity of the medullated and frequently very thick primitive fibres with the salivary cells may often be easily demonstrated. I have seen this occur in a great variety of modes, and in the clearest manner in the salivary glands of the ox and rabbit (submaxillary and parotid glands) (figs. 107 and 108).

In completely isolated preparations (figs. 106 and 108, A B) it may be

observed that the white substance of Schwann ceases as though suddenly cut off at a short distance from the salivary cells, and that the nerve appears as if adherent to the soft protoplasm of the epithelial cell.

If the point of attachment be examined with very high magnifying

Fig. 104.

Fig. 104. From the Rabbit. Medullated fibre blackened by perosmic acid. Magnified 500 diameters.

powers, it will be seen that immeasurably fine fibrils proceed from the nerve, which pass directly and without interruption into the fibrils of the protoplasm of the salivary cells. This appearance is most beautifully presented if the medullated fibre be deprived of its medulla by pressure. There then remains a pale fibre composed of extraordinarily fine fibrils, which are

Fig. 105.

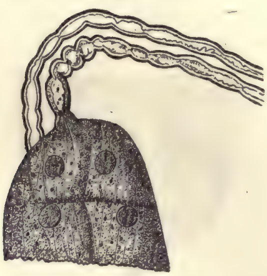

Fig. 105. From the Rabbit, after maceration in iodized serum, showing the termination of a medullated nerve in an alveolus. From the submaxillary gland. Magnified 590 diameters.

directly continuous with the fibrillated substance of the epithelial cells. This character is especially important, because it constitutes a clear evidence of the absolute continuity and fusion of the axis cylinder and epithelial cell. As I have not seen any fibres blackened by perosmic acid upon the membrana propria, though both the blackening and the medulla may constantly be seen extending to epithelial cells in well-isolated preparations, I must conclude that ordinarily the mode of termination in the alveoli is that the nerve perforates the membrana propria, and enters directly into the superjacent salivary cells. The nerve medulla consequently terminates at the cell. That point of the salivary cell where the nerve enters is marked

by a slight increase in the transparency of the protoplasm, and this portion occupies a segment made up of from one-fourth to one-third of the spherical volume of the cell (fig. 108). I have not seen the nucleus in this segment, but in the remaining more darkly granular portion. The nerve tears across with remarkable facility at the point of its insertion, which appears to be extremely soft, and hence leaves no trace of the point at which it was attached to the cell. This may be reasonably attributed to the fact that

Fig. 106.

Fig. 106. Termination of a branching fine medullated fibre in the salivary cells of an alveolus. From the submaxillary gland of the Ox, the nerve blackened by perosmic acid. Magnified 490 diameters.

the connection is only effected by means of the axis cylinder, which, whilst it is continuous with the semi-fluid protoplasm of the cell, undergoes no sudden interruption at this point. It is on this account impossible, without appropriate, though necessarily very slight, hardening with reagents, to

Fig. 107.

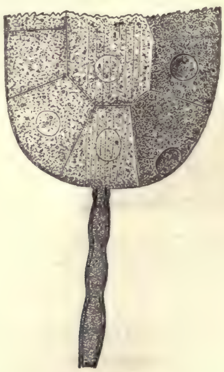

Fig. 107. Termination of a medullated fibre of average thickness in the large salivary cells of an alveolus. From the submaxillary gland of the Ox. The nerve has been blackened by perosmic acid. Magnified 500 diameters.

bring into view the isolated fresh salivary cells, with their associated nerve fibres. It is not surprising that the medullated primitive fibres are sometimes very fine, sometimes very thick, when we know that the epithelial cells gradually increase to substantial structures, from minute nodules on

extremely fine axis-cylinder fibrils. With their increase the size of the nerve also augments; it acquires a medulla, and becomes progressively thicker. It is this circumstance in part, and partly the fact already mentioned, that, on the application of pressure or other form of mechanical violence, the medulla separates from the dark-edged primitive fibres, whilst the axis cylinder breaks up into fibrils penetrating the protoplasm of the salivary cells, that forbids us any longer to regard the latter mode of nerve termination as peculiar.

Fig. 108.

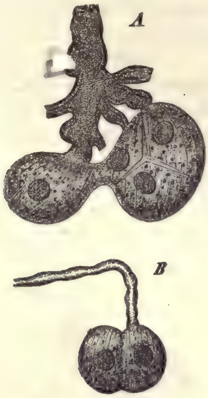

Fig. 108. Termination of medullated fibres treated with perosmic acid in isolated salivary cells. A, thick branched fibres distributed to large salivary cells; B, fine nerves distributed to smaller salivary cells. From the submaxillary gland of the Rabbit. Magnified 590 diameters.

Fig. 109.

Fig. 109. Multipolar nerve cell. From the Rabbit. Magnified 80 diameters.

Whether this holds for all pale nerve terminations found in the alveoli appears to me, from the stand-point obtained in the physiological experiment demonstrating that two kinds of nerves exert an action upon the gland, to be doubtful. There may in particular be found well-preserved

long tubes, apparently composed of connective tissue, the wall beset with nuclei, continuous with the membrana propria of the alveoli, and containing one or more fine fibrils, that are lost in the gland vesicles. They rarely occur in comparison with the medullated fibres, but are more stable on account of their sheath, so that they alone can be seen in some of the modes of preparation, on account of the fluidity of the medullated fibres.

II. On the mode of Nerve Termination effected by Multipolar Cells.—I have elsewhere described small pale cells (fig. 109) possessing numerous processes adherent to the alevoli, and for the most part smaller than the salivary cells. I regard these as nerve cells, and consider them as entering into communication, not only with the salivary cells, but also with the nerve fibres.

All later inquirers (Kölliker, Boll, Heidenhain) have with remarkable unanimity and with great precision described these multipolar cells as indifferent structures *forming a reticulum*, and properly to be regarded as

Fig. 110.

Fig. 110, A, B. Multipolar cells in connection with salivary cells. Magnified, A, 480, B, 590 diameters.

C. Peculiar cells with round thick processes, and containing refractile fat particles. Magnified 590 diameters.

belonging to the connective tissue. According to Kölliker and Boll, these cells constitute the membrana propria, which I have already described.

The above-named inquirers silently assume that the opinion I hold of the direct continuity of these multipolar cells with the glandular epithelium, by means of thick and anatomosing fibres, is erroneous. Boll was unable to discover these communications, but refers to *apparent* connections, and is of opinion that the multipolar cells, with their intercommunications, in some instances closely resemble salivary cells, so that the possibility of a false impression is conceivable.

But as I am satisfied that I have seen the connection of the multipolar cells with salivary cells, I hold it to be my duty, especially on account of the importance of all that depends upon it, to prove this point with the most rigorous scientific accuracy. As I have more recently on many occasions observed such connection, I may remark that we are here engaged with the examination of completely isolatable cells, which communicate with one another by means of a thick anastomosis, and the two points of attachment of which may be seen in perfect profile (fig. 110, A B C). One of these cells is pale, striated, with many radiating processes, and with the body almost entirely filled with the nucleus (fig. 110, B). The other is round or slightly polygonal, with abundant granular protoplasm and a relatively small nucleus.

As the observations were made upon rabbits, the fully developed salivary

cells of which have so stereotyped an appearance, I regard it as absolutely impossible that I should have mistaken any other cell for a salivary cell. Moreover, I have actually seen the connection whilst the salivary cells in question were still adherent to others, and forming part of the characteristic mosaic (fig. 110, A and C).

It follows therefore that the multipolar cells cannot be connective tissue cells, as maintained by Kölliker, Heidenhain, and Boll; for the true salivary cell is an enlargement of a medullated nerve. It cannot, consequently, give off any process which is a connective tissue fibre, or which is continuous with connective tissue cells; for between animal tissue and connective tissue substance there cannot be any continuity of substance.

Inasmuch as I am now satisfied that the multipolar cells are continuous through their processes with nerve fibres (fig. 109), it follows that they must either be modified epithelial cells or ganglion cells. Their continuity with nerve fibres does not decide the question, since the salivary cells also present this character under the most various modifications in common with true nerve cells.

There consequently remain, as means for determining the point, only analogy and anatomical structure. To whatever degree the multipolar cells may differ amongst themselves in their size and form, and in the characters of the nucleus and of the protoplasm, as indeed was observed by Boll, they nevertheless resemble nerve cells more closely than epithelium, as is shown by the fact that small ganglion cells have been admitted to occur amongst them by various observers, as by Henle and Krause. In the next place, in regard to the great variation that they present, it is important to remember that if the alveoli, as we have decisively proved, undergo continuous regeneration and disintegration, the nervous tissue must be subject to similar metamorphoses. The nucleus in some of these remarkable cells is round, as was also observed by Boll; and is at the same time transparent, and almost entirely fills the cell. This peculiarity is presented also by other peripheric ganglia, as the granules of the rods and cones of the retina, which unquestionably represent bipolar nerve cells. Moreover these cells exhibit a pale striated protoplasm, the fibres of which may be followed into the similarly striated, and in parts highly refractile, cylindrical processes. Such cells consequently, taken as a whole, exactly resemble, and would be held by all to constitute, ganglion cells.

Besides these, we find other cells with ellipsoidal or flat nuclei, which are partly round and partly present flat processes and membranous cell substance, and are quite transparent. Finally, there are still others, lying within the young alveoli, which possess granular soft protoplasm in sparing quantity, contain round highly refractile nuclei, and possess numerous cylindrical highly refractile processes. These are undoubtedly in an early stage of development (fig. 110, C). Even if these cells form a reticulum, this furnishes no evidence of their indifferent nature, since all ganglion cells are beyond doubt parts of the great network of animal tissue.

Lastly, even if, looking at the great variety of multipolar cells, it be admitted that we are here dealing with cells of different nature and attributes, it still appears to me that we have obtained a sufficient answer to one of the above alternatives, and that the multipolar cells must be regarded as small ganglion cells.

The mode of termination of the nerves here described I have termed that "effected by the means of multipolar cells," an expression which is

only in accordance with fact, and to which, consequently, no objection can be raised.

The remarks hitherto made upon the relation of the nervous system to the salivary glands refer exclusively to the submaxillary gland.

At the same time I have convinced myself that the alveoli of the parotid gland enter into relation with strong medullated nerves in the same manner as has been just described in the case of the submaxillary gland. The parotid, moreover, as well as the sublingual gland, possesses salivary tubes presenting similar structural features. Krause has demonstrated the presence of similar multipolar cells in the parotid, and I have also more recently found them in the sublingual gland. If we take into consideration the very similar structure that is thus exhibited by these glands, and the dependence of their activity upon the nervous system, we can scarcely hesitate to believe that a complete agreement prevails also in regard to the mode of termination of their secretory nerves.

As regards the sensory elements of the nervous system, W. Krause * has discovered a simple kind of Pacinian corpuscle, to which he has given the name of "Terminal Gland Capsules." In the majority of animals, however, they are rarely present.

Fig. 111.

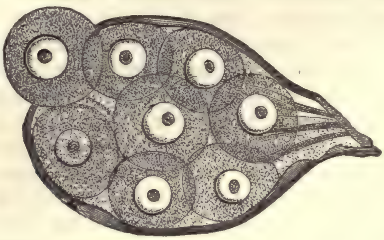

Fig. 111. Ganglionic knot from the submaxillary gland of a Rabbit. Magnified 480 diameters.

The structure of the larger ganglia which are found in the course of the nerve fibres and trunks still remains to be considered. The ganglion cells occur partly isolated and partly in groups which accompany the nerve cords for a considerable distance, or form roundish knots enclosed by a dense sheath of connective tissue. These knots attain the size of 0·060 millimetre and more. The nerve cells lying in their interior (fig. 111) have a diameter of 0·028 millimetre, with a nucleus of the diameter of 0·012, and a nucleolus of 0·002 millimetre in diameter.

We meet also with much smaller ganglion cells, which are not larger than salivary cells, with a diameter of or about 0·014 millimetre. The cells accumulated in one group do not materially differ from one another in their general magnitude. The ganglion cells include a spheroidal or oval, transparent, delicate, but sharply defined nuclear vesicle, and when in their fresh state their protoplasm is very delicate and confusedly granular.

In the smaller forms the cell contents are sometimes rather more granular, but the nucleus is always as clear as water. The groups are constantly in connection with afferent and efferent nerve fibres. In some instances a sin-

* *Zeitschrift für rationelle Medicin*, Band xx., p. 60, 1849.

gle ganglion cell is found in the course of a fibre of Remak. It is remarkable that a large ganglion cell of this kind, having a diameter of 0·042 millimetre (see fig. 112), may contain several nucleoli; and moreover, at the point of transition into the nerve fibre, may present a slight deposit of protoplasm, with several ganglionic nuclei; and I desire especially to direct the attention of observers to this singular form of ganglionic substance. The relations of the ganglion cells of the gland are also deserving of special investigation, which will certainly bear on the physiological point of whether the sympathetic is distributed exclusively to the bloodvessels, or whether it does not stand in intimate relation to the secreting cells.

Fig. 112.

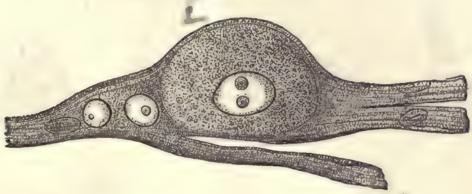

Fig. 112. Solitary ganglion cell with a deposit of nucleated ganglionic protoplasm. From the submaxillary gland of the Rabbit. Magnified 480 diameters.

§ 5. The Regeneration of the Glandular Epithelium.—I have already called attention, in my work on "The Termination of the Secretory Nerves in the Salivary Glands," to the alveolar-like small projections or bud-like processes of the so-called excretory ducts, and have there expressed the opinion that, both in the primary embryonal development of the gland, as well as in the adult, new salivary cells and alveoli develop from the salivary tubes. I am now in a position to describe the process with accuracy.

If the salivary tubes isolated by any of the ordinary modes, or sections of them, after the action of hardening agents, be carefully examined for the brush-like processes of the cylindrical epithelial cells, it is easy to observe that the fibrils in various salivary tubules, or even in separate sections of the same tube, may present a very different appearance. As a general rule, even with the highest powers, they appear as immeasurably fine varicose fibrils (fig. 96). But all conceivable intermediate or transitional forms may be met with, up to moderately thick fibres (0·001 millimetre) (figs. 113 and 114). In proportion as they increase in size they lose their soft pale appearance, acquire high refractive power, which begins to be apparent at the free extremity of the cylindrical cells, and gradually extends towards that extremity to which the fibres are attached. The end of the fibre frequently breaks up into several filaments, so that groups of branched processes appear to have budded forth from the columnar cells, which often form thick brushes, the base of which is formed by the small columnar cell. In the next place, the free extremity of these fibres is enlarged into a kind of head, resembling a small club, that forms a minute corpuscle (fig. 114). These clavate extremities may be seen to increase in size till they are clearly distinguishable as cell nuclei, surrounded by a sparing quantity of protoplasm. This process of formation of nuclei commences from infinitesimally small points in the fibre, and extends towards the columnar cells, so that two, three, or even very many may originate in one fibre. The small clavate extremities gradually enlarge to form salivary cells, and after a time it is not difficult to find

such epithelial cells constituting the mosaic-work of the alveoli, and directly continuous with the columnar cells by means of processes (fig. 114, E). Usually the processes are of such a form that the fibres of the brush attached to the columnar cell increase in size as they recede from it, and develop a very delicate protoplasm, in which larger or smaller nuclei are contained.

Fig. 113.

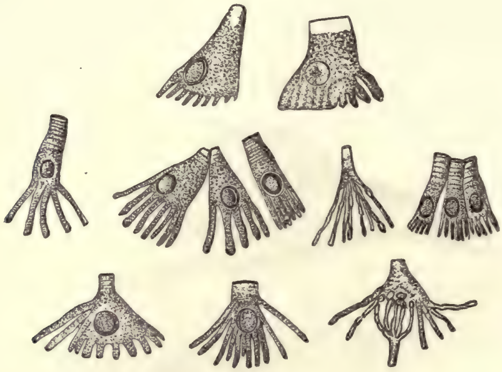

Fig. 113. Cells. From the submaxillary gland of the Rabbit, after maceration in iodized serum. Magnified 590 diameters.

Fig. 114.

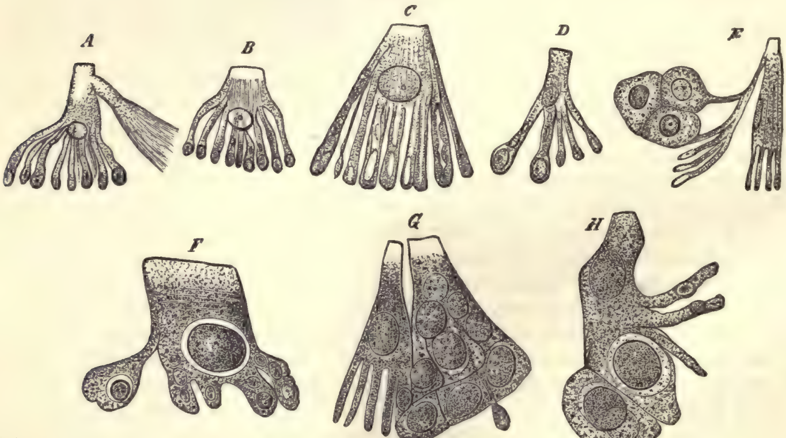

Fig. 114. A, B, C, D, E, isolated cylindrical cells with processes containing nuclei. A, B, D, E, magnified 590 diameters; C, magnified 1,200 diameters. F, G, H, cylindrical cells with processes, which are evidently young cells, and form at G a beautiful mosaic. Magnified 1,100 diameters.

Since it always occurs that a large section of a salivary tube is implicated in this remarkable process of cell formation, and since the most active growth takes place upon the membrana propria, the wall will be found to be

enormously thickened and laminated, with primary and secondary projections, whilst the young cells enlarge and arrange themselves in the form of a mosaic. But coincidently the connective tissue projects inwardly into the thick wall, separating off the cells into alveolar-like groups. I have observed this process of the projection of alveoli *en masse*, as it were, from the salivary tubes of a columnar cell, particularly well in the sublingual gland of the rabbit. The degree of ripeness which the various cells contained in one alveolus exhibit is not always the same; thus it is customary to meet with a few young cells at the periphery of the alveoli in mucous glands (such as the submaxillary of the dog, ox, and rabbit). How is this process of new formation of salivary cells to be explained? They are formed in the processes of the columnar cells, without the nucleus being in any way implicated; for, even when these processes contain numerous nuclei, the nucleus of the columnar cell still appears to be always perfect, spherical, sharply defined, and without a trace of gemmation. Even with the highest magnifying powers I have never observed any indications that a filament was given off from the nucleus which could serve as a point of origin for the young nuclei. A few processes even pass over the nucleus through the columnar cell, and their striæ run parallel to its axis as far as to the free surface directed towards the cavity of the salivary tube, so that it scarcely appears to be possible that the nucleus originating in the extremity of such a process could be derived from the nucleus of the cylinder cell. The latter is almost always single, rarely double. Very small and non-nucleated columnar cells, possessing processes that are filled with small nuclei, are also sometimes present (fig. 113). As as on this ground I do not feel myself justified in attributing

Fig. 115.

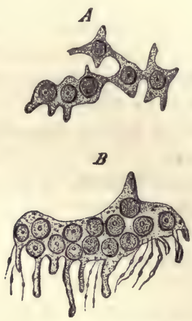

Fig. 115. Multiplication of nuclei in the dilated and swollen processes of the columnar cells. A, formation of small multipolar cells; B appears to be a dilated process of a columnar cell. Magnified 590 diameters.

the origin of the new nuclei developing in the processes to that of the columnar cells, we must admit that we have before us a case of free cell formation, if under this term we understand that mode of cell increase in which the newly developed nucleus originates independently in a cell, and is not a morphological element proceeding from a division of a previously existing nucleus. When we see the axis cylinder and its fibrils to be directly continuous with the fibrils of the columnar cells, without any difference being perceptible between the axis cylinder and the fibrils of these cells, we may legitimately describe the nerve as extending to the point where it joins the

substance of the body of the cell. That is the most natural explanation that can be given. This explanation, however, possesses the greatest significance in regard to the mode of development of the glandular epithelium, because it directly follows that the young nuclei originate in the axis cylinders, and that the gland cells which at a later period seem to constitute a thickening of the axis cylinder bud forth, as it were, from the nerves. This explanation renders it intelligible why the nuclei of the columnar cells are so indifferent during the multiplication of the epithelium. In opposition to this view, which I regard as the most probable, it may be urged that, in consequence of the intimate fusion of nerve substance and epithelium at the periphery, no sharp limit can be drawn, showing where the one ceases and the other begins; and that, moreover, it is probable that imperceptibly fine processes are given off by the nucleus of the columnar epithelial cells, which become detached at an early period by fission. That the nuclei of the salivary cells have processes, cannot, however, be regarded as forming a valid objection to my view, since the young nuclei may really be thickenings of the axis-cylinder fibrils.

I may further adduce, as a weighty argument in favor of my view, that the fibrils of the axis cylinder do not terminate at the surface of the fully developed salivry cells, but, as in the case of the ganglion cells, may be traced into their very substance.

Now, since the finest axis cylinders and fibrils extend to the columnar epithelial cells, and are connected with the processes that are in course of development, and since portions of these processes subsequently become large salivary cells, connected with thick medullated nerve fibres, it follows that the nerves must increase coincidently with the young epithelium to which they belong. Amongst these metamorphoses there also occurs a mode of termination of the medullated nerves, to which I some time ago called attention, and which consists in the nerve suddenly undergoing frequent division, then enlarging, and containing finely granular protoplasm, with many nuclei of various sizes. I have named this mode of nerve termination, that by a "protoplasmic foot." If, as I have sometimes observed, many of the nuclei appear to be provided with fibres, which can be followed into the interior of the nerve fibres, it is highly suggestive of the development of the gland cells from the nerves.

In regard to every explanation it must be observed that transitional forms may occur, respecting which it is impossible to say whether they are epithelial or nervous. The continuous and luxuriant neoplastic formation taking place in the substance of the salivary ducts presupposes their regeneration, respecting which I have formed my own opinion, but have arrived at no definite conclusion. In like manner the persistent neoplastic formation of the alveoli in adult animals determines an atrophic detachment of those already present. In Moles I have sometimes found the alveoli with pale offshoots of various forms, and pale finely granular contents, which may be such atrophied and separated alveolar segments.

I first comprehended the complexity of all forms of salivary glands when I recognized the constant production and disintegration taking place in them, which is referrible to the nerve substance.

§ 6. The Morphological Constituents of the Saliva.—Healthy saliva contains no morphological elements, but forms a transparent perfectly homogeneous fluid. But when the mucous membrane is irritated, either by ligature of the excretory duct, or by the introduction of a canula into its interior, we obtain isolated morphological elements, which are continuously

developed by a kind of catarrhal condition and exudation. The appearance of these has led some observers to the belief that normal saliva contains formed elements, and continually carries off glandular epithelium. As recent investigations have been in direct contradiction to these statements, I may perhaps be allowed briefly to state the grounds on which my opinions are based. When, in a dog, the duct of Wharton and the nerves supplying the submaxillary gland have been exposed, isolated, and divided, a watery saliva flows from the duct, as transparent as a dewdrop. The secretion found in the duct is also clear. If a canula be now introduced, and firmly tied in, and the nerves be irritated, the fluid immediately becomes cloudy; but when a few drops have been discharged, it again resumes its transparency. The first drops discharged on irritating the nerves, after the introduction of the canula, are those which were already in the duct, and were originally transparent, but have become cloudy whilst still in its interior, for the clear secretion extracted from the freshly excised ducts remains clear when exposed to the air. Contact with the wall of the duct has consequently rendered the secretion cloudy. If we examine the first drops microscopically, we shall find they contain isolated cells and groups of epithelial cells with nuclei, unquestionable modulated nerve fibres, connective tissue, etc.; in a word, constituents which have been detached from the mucous membrane of the duct by the canula, and which there is no object in describing further. As soon as a stronger salivary current is induced by excitation of the chorda tympani, these detached elements are completely washed away, the fluid again becomes quite clear, and no longer contains any morphological elements. After a short time, however, they reappear in sparing number as the so-called salivary corpuscles, that is to say, as small, finely granular, nucleated cells, presenting in some instances amœboid movements, whilst the fluid is rendered cloudy by the presence of fine granules. These bodies, however, it may be easily shown, always proceed from the wall of the ex traordinary duct after it has become affected with catarrhal inflammation, and not from the gland; for if the nerves are irritated sufficiently long to cause a flow of perfectly clear saliva from the india-rubber tube of the canula, and the excitation be then interrupted for ten minutes, and, before it is recommenced, the saliva stagnating in the caoutchouc tube from the previous irritation be pressed out, it will be found, when collected, to be as clear as before. If the excitation be now reapplied, we obtain, since the canula is of very small diameter, for the first three or four drops, that which has collected in the excretory ducts from the previous irritation. These three drops are quite cloudy from exudation and detached cells, but are followed immediately by saliva as clear as water; that is to say, as soon as the exudation has been washed out of the duct. I have estimated the capacity of the duct from the canula to the gland, and am of opinion that it will contain about three drops. The quantity is certainly very much smaller than the total secretion which, in the period before the renewed excitation, stagnated in the very numerous and, in some instances, very wide ducts. Thus it appears that the originally clear saliva contained in the duct has become cloudy, and obviously in consequence of a pathological process; for, if a freshly exposed duct be emptied of its contents, even if the dog have previously discharged no saliva, the secretion obtained on section is clear.

The saliva caused to flow by irritation of the sympathetic nerve contains a large number of spheroidal particles of mucus, together with morphological elements of a less clearly definable nature, but representing products of disintegration. Heidenhain, however, was frequently unable to discover any morphological elements. As this kind of saliva can only be obtained

in small quantity, the exudate that is poured forth may perhaps never be completely washed out and evacuated, and as only a small quantity of saliva appears at long intervals, the fluid essentially consists of this. Heidenhain has shown that when the excitation is long maintained it becomes clearer. The relations of the sympathetic nerve to the salivary glands are, however, involved in much obscurity.

From what has now been adduced, it will be seen that further observations are required before it can be admitted that the saliva naturally contains formed elements.

§ 7. Of the Alteration of Structure in the Glands caused by the Performance of their Functions.—When the salivary glands have been long in action, they become lighter, softer, paler in appearance, and both absolutely and relatively poorer in solid constituents. After being long at rest the inverse changes occur, and they assume a yellower color. This last I believe to be occasioned by the accumulation of numerous molecules in the salivary cells. The gland becomes "charged." Heidenhain has recently expressed the opinion, that in some animals (Carnivora and Herbivora) the secretion is accompanied by the disintegration of a certain proportion of salivary cells, the place of which is supplied by a new generation developed at the periphery of the alveoli. In rabbits, the secretion of saliva in the submaxillary gland is effected, according to Heidenhain, exceptionally without demonstrable *disintegration and neoplastic cell formation.*

The important and novel principle in respect to the action of the nerves, established by the observer just mentioned, cannot be here passed over in silence. I have placed an investigation into the accuracy of his statements into the hands of my pupil, Herr Anton Ewald, of Berlin, who has been for some time engaged under my superintendence with the structural changes induced by excitation of these glands, and has pursued precisely the same method as that adopted by Heidenhain. After one submaxillary gland had been excited for a considerable period (as long as for seven hours) whilst the other had been kept at perfect rest, both were removed from the living animal, and from these thin sections were made with a razor, which were immediately thrown into a large quantity of absolute alcohol. By this means we avoided, as far as possible, in the unexcited gland, which is charged with mucus-forming substance ("mucigen"), the production of any material structural alteration through the *post-mortem* formation of mucous vesicles in the alveoli, consequent upon displacement of cells and protoplasm. This precautionary measure was not unnecessary; for in the gland, which has been for a long time actively discharging its function, no more "mucigen" is contained, and therefore, in this case, no alteration of structure can occur from the formation after death of mucous vesicles.

When both glands had been hardened for an equal time in alcohol, very fine sections were prepared, macerated for the same period in the solution of carmine in glycerine, employed by Heidenhain, and finally, after the most careful washing, examined in glycerine. It is obviously a matter of great importance that the sections should be made as fine as possible, and all those that are thicker than the diameter of a salivary cell should be rejected. If the cell mosaic lining the interior of the alveoli of the quiescent gland be examined, we find for the most part a single layer of *sharply defined transparent* polygonal cells flattened by mutual pressure, which, however, are not perfectly hyaline, but exhibit a delicate *striation*, as though a perfectly transparent substance were traversed by numerous extremely fine pale fibrils. These salivary cells, which, on account of their contents con-

sisting in the Dog chiefly of mucus, with but little albumen, Heidenhain has termed "mucous cells," are more or less, though in general but slightly, tinted with carmine. When the staining is more strongly marked, the cells contain albumen. A structure, which is probably the nucleus of the mucous cell, lies together with a little protoplasm at the periphery of the alveolus, and resembles the process of the cell in being stained of a deep red color. Inasmuch as all the processes, together with the nuclei and the protoplasm, are situated at the periphery of the alveolus, a broad red zone is here frequently formed. Here and there one or more salivary cells appear more or less deeply tinged with carmine. These cells are named by Heidenhain the "crescent." He regards them as the earlier stages of development of the cells which gradually become "mucous cells," which, I think, is not improbable. He silently acquiesces in the view I have stated above, that all salivary cells do not behave in the same manner with reagents, a difference that I am disposed to attribute to their various grades of development.

If we now consider the excited gland, the differences which present themselves are, that *all the cells are stained with carmine*, though perhaps only slightly, some being more strongly tinted than others—the staining, however, independently of the protoplasm, being, on the whole, less marked than in the quiescent gland; that no evidences of *multiplication by fission* of the young cells at the periphery of the alveoli are visible, in corroboration of which I may refer to Plate i., figs. 84 and 85 of Heidenhain's Essay; that *all the contour lines* are remarkably pale and softened off, especially those separating the alveoli and the salivary cells, which are *no longer defined by thick lines*; that the nucleus is *less* reddened, *more delicately* contoured, *larger*, and, generally speaking, *spheroidal*. The effects of the excitation consequently are, that instead of cells *not becoming stained with carmine*, with round nuclei *shrinking* in alcohol, and becoming intensely stained with carmine, we obtain cells *reddening* with carmine, containing nuclei which undergo *no shrivelling* in alcohol, and are less deeply stained with carmine.

Heidenhain draws the conclusion from these facts, that the first form are disintegrated in the act of secretion, whilst the second are newly developed.

There still remains the possibility that the "mucous cells," in consequence of their persistent activity, have undergone an essential alteration in their chemical constitution, to which the differences in their appearance are attributable, according to whether they have been at rest or long in action. I cannot, however, deny that the completely different appearances (see fig. 115) presented, strongly support Heidenhain's opinion.

Heidenhain lastly adduces, in support of his opinion, the circumstance that he was able to isolate a larger number of cells undergoing fission from the excited gland, after maceration in iodized serum, than in that which has been kept at rest. The epithelial cells of the salivary glands of the dog are generally isolated with difficulty. The isolation of the younger cells in the excited gland may perhaps be facilitated by this very excitation rendering them looser, softer, and more watery, as Heidenhain himself remarks. May not also the continuous streaming of saliva, rich in the corroding carbonate of soda, favor their isolation? It is further noticeable that, according to Heidenhain, these young cells, after long maceration, become isolated sooner than other kinds of epithelia, showing that, under favorable circumstances, they are formed earlier or in larger numbers. I must further observe, that, in accordance with my experience, I can demonstrate in every quiescent salivary gland thousands of epithelial cells in the act of multiplication. The sublingual gland of the rabbit is particularly well adapted for this purpose, offering the additional advantage that, like the submax-

illary gland of the dog, it exhibits large and beautiful mucous cells and semi-lunar bodies. In any such gland, thousands of young epithelial cells, developing by the process of gemmation, may be discovered. I hold a gradual process of disintegration of the alveoli to be highly probable, on the ground of that regeneration of salivary cells which I discovered to proceed from the cylinder cells of the excretory ducts. The question as to how far the nervous system exerts a primary or a secondary influence on this vegetative process still demands further investigation.

§ 8. The Stroma of the Salivary Gland.—The connective tissue consists partly of membranes, partly of fasciculi of fibres, which form a porous network traversing the whole organ, and are commingled with a larger or smaller number of elastic fibres, that are often developed to a very large extent. The nuclear structures are not in general readily demonstrable, but when present, appear as small oval, sharply defined, highly refractile corpuscles. In some places, finely granular nucleated cells are found, with thick processes, which must, in all probability, be also regarded as amongst the cellular elements of the connective tissues. As we have already mentioned, pale, flattened connective tissue cells form, according to Boll and Kölliker, a reticulum around the alveoli.

In regard to the presence of the muscular fibres that Schlüter states he has seen in the stroma, I beg to observe that I have recently directed my especial attention to the determination of this point, which on physiological grounds is of great importance; and that in sections of the gland which had been stained with carmine, hardened in alcohol, and examined in glycerine, I have been able to satisfy myself of the presence of, in some instances solitary, in others of fasciculi of smooth, fusiform muscular fibre cells, with elongated rod-like nuclei, that certainly could not be regarded as constituents of the vessels, and must confer some, though perhaps only slight, contractility on the stroma.

The connective tissue stroma intervening between the alveoli attached to a single excretory duct is exceedingly small in quantity, so that the alveoli lie closely compressed and flattened against one another. The several grape-like masses of glandular substance belonging to different small excretory ducts are separated from one another by broader bands of connective tissue, in which, when the animals are fat, fat cells are seen, resulting from the conversion of connective tissue cells, so that treatment with perosmic acid brings into view a delicate marbling, formed of black lines, in every fresh section of a gland. Where the secondary and tertiary groups of grape-like glands belonging to a larger excretory duct are united into a compact mass, numerous lobules are formed, visible with the naked eye, and divided from one another by fissures. The walls of these fissures are composed of connective tissue fibres, and I have observed them to be lined by an indistinct endothelium. Nevertheless, I have, up to the present time, found no functional peculiarity connected with these structural features. I do not in the least doubt that the fissures belong to the lymphatic system, as Gianuzzi maintains. Nothing definite is known in regard to the anatomy of the bloodvessels, which stand in such a remarkable relation of dependency to the nervous system, nor yet in regard to the lymphatic vessels. The capillaries wind around them in close contact to the membrana propria, forming a very close plexus, derived from different quarters, and show no points of difference from the ordinary arrangement.

§ 9. Mode of Investigation.—If it be desired to obtain a general view

of the arrangement of the alveoli, excretory ducts, cells, and stroma, fine sections should be made of hardened glands. The hardening is best effected by placing thin portions, whilst still warm from the body, in absolute alcohol. Fine sections can then be made, tinted as usual with carmine, and exam-

Fig. 116.

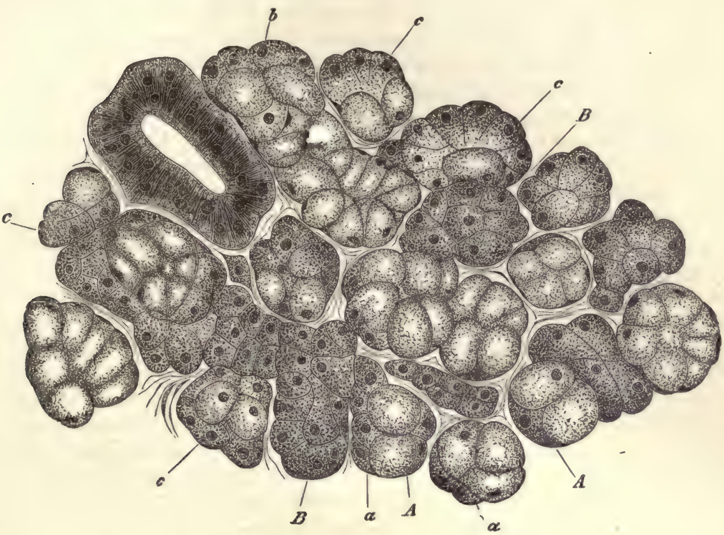

Fig. 116. Quiescent gland.

Fig. 117.

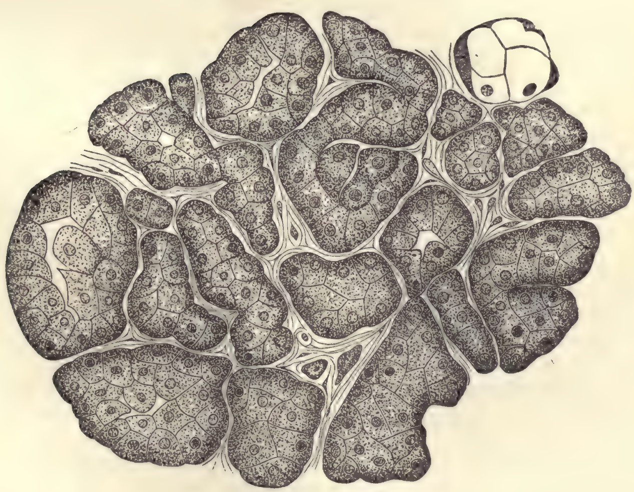

Fig. 117. Exhausted gland from the Dog, after Heidenhain.

ined in glycerine. In order to study the finer structural relations, every method of hardening must be avoided. Sections made with very sharp knives of the perfectly fresh gland, can be examined in iodized serum, or in chromic acid containing from 25 to 50 per cent., to which a little iodized serum has been added. When thin sections, thus made, are carefully broken up with needles, isolated alveoli may be obtained, with salivary tubes, epithelial cells with nerve terminations, and the like. The isolation of the epithelial cells is best effected by the application of iodized serum, in which the gland has been allowed to macerate for from four to six days, or still better, by treatment with iodized serum, subsequent to maceration in chromic acid of one-half per cent. The chromic acid macerates the glands most advantageously, if one or two glands have previously been lying in it for one or two days. When quite freshly applied, the volume of this reagent should not exceed from two to four times the volume of that of the gland. Another method of isolating the elementary constituents, especially of the glands in the rabbit, consists in placing the latter in a small test tube, and adding from four to eight drops of solution of chromic acid, containing one-fiftieth per cent. After the course of an hour, when the organ appears hardened and translucent by imbibition, fine sections may be prepared and broken up by fine needles in the same solution. Solution of caustic alkali, containing 33 per cent., is also well adapted for the isolation of the elementary parts. As soon as the gland has become brown, which occurs in a quarter or half an hour, the tissue can be easily broken up. The liquid in which the preparation is examined, it is obvious, must not be water, but always the same solution of alkali. A method especially adapted for the demonstration of the mode of nerve termination is that introduced by Max Schultze, which consists in laying the fresh gland in perosmic acid, and thus staining the medullated nerves of a dense black color, causing them to resemble tubes injected with ink, whilst the epithelial cells, examined in thin layers, are scarcely, if at all, colored. The salivary tubes only assume a brownish tint.

CHAPTER XV.

STRUCTURE AND DEVELOPMENT OF THE TEETH.

By W. WALDEYER.

Hardened structures of the animal organism, similar to those which are called teeth, though certainly presenting very various histological structure, are found widely distributed both amongst the vertebrate and the invertebrate series.

With the exception of the larval form of Petromyzon (Ammocœtes); of Amphioxus, Accipenser, and the Lophobranchii (Cuvier), amongst Fishes; of some Toads (Pipa), amongst Amphibia; of the Chelonia, amongst Reptiles; of the entire class of Birds; and of the Myrmecophaga, Manis, and Echidna, amongst the Mammals, all vertebrate animals possess teeth. In the whalebone Whale they are present in the fœtal state.

The anatomical model of a tooth of a vertebrate animal is a large papilla of the mouth or of the pharyngeal mucous membrane, which, in consequence of chemical and histological conversion of its constituents, has acquired a remarkable degree of hardness. And, according to whether the connective tissue substance of the papilla participates in the hardening or not, two large groups of teeth are distinguished—dentinal teeth and horny teeth.

The horny teeth are by far the most simple in their structure. They appear as more or less developed papillæ covered with a thick horny investment. They are never continuous with portions of the skeleton, but constitute the transition to other horny formations, as hairs, stings, etc. True horny teeth are met with in the Petromyzidæ, the Myxinoids, and in Ornithorhyncus. The whalebone of many whales, and the horny masticating plates of Rhytina Stelleri, though remarkably complex structures, yet clearly belong to the same series of formations.

In the dentinal teeth the connective tissue matrix of the papilla plays a most important part in the hardening process, which here proceeds in a manner precisely similar to the ossifying process, except that no true bone is formed, but only an allied substance of much harder consistence, and differing more or less in histological structure, termed *dentine*. The epithelium of the tooth papilla either atrophies to a rudimentary horny investment, the *cuticula* (membrane of the enamel), or it becomes elongated in a remarkable manner into long petrified prisms, which collectively invest the dentine, and are known as the *enamel*. In addition to these there is found an accessory structure, the *cement*, a true bony substance, which especially invests the fangs of the teeth. Dentinal teeth are constantly attached to the parts of the skeleton surrounding the mouth and pharynx, and for the most part to the lower jaw.

From the simple arrangement of the three chief constituents of the teeth, as they occur in man, for example, there are manifold and complex variations. Amongst these may be enumerated in particular the so-called folded enamel teeth of Rodentia, Solipedes, and others, and the compound teeth of many fishes and fossil reptiles (Labyrinthodon), of the elephant, etc. The "folded enamel" teeth, dentes complicati, are

formed on the type of a simple tooth. The dentine of the crown is, however, folded like a ruff, and the enamel and cement dip in to form a covering to the surface of all the sinuosities. Of the dentes compositi two principal forms can be distinguished. In one, a common stem or trunk is present, which gives off a number of separate toothlets (Galeopithecus, Labyrinthodon), whilst in the second a common tooth pulp is absent, and instead we find, as in many fishes and Orycteropus, numerous independent toothlets proceeding from the jaw, and united to form a common tooth. The pulp of the teeth

Fig. 118.

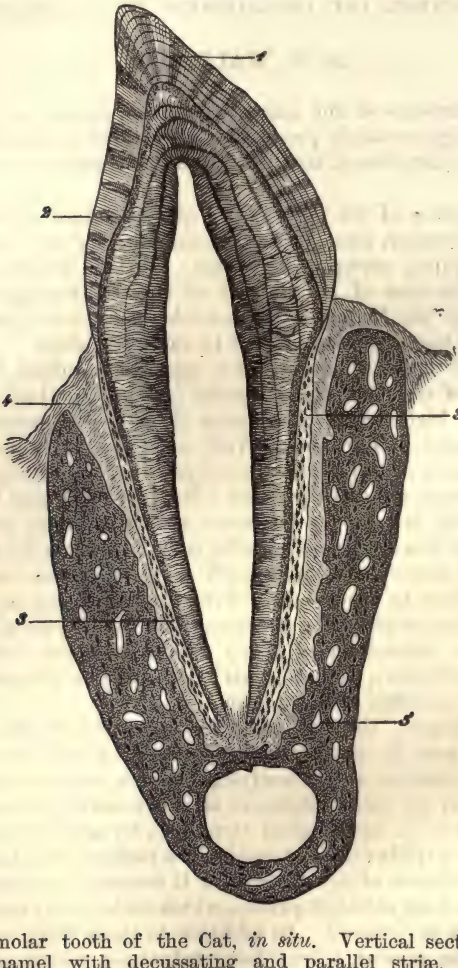

Fig. 118. Premolar tooth of the Cat, *in situ*. Vertical section, magnified 15 diameters. 1. Enamel with decussating and parallel striæ. 2. Dentine with Schreger's lines. 3. Cement. 4. Periosteum of the alveolus. 5. Inferior maxillary bone.

of the Labyrinthodonts is therefore comparable to the compound filiform papillæ of the tongue; whilst the true compound teeth of the second class bear the same relation to simple teeth that the hoof does to hair. The several back teeth of the Elephant have the characters of the first kind; each separate tooth, however, presents folding of the enamel, so that a highly complex structure results.

On the other hand, the structure of a tooth may be simplified by the absence of one or two of the above-mentioned dentinal tissues, especially the enamel, or the enamel

and cement. Thus the tusks of the Elephant and the teeth of the Edentata have no enamel; and again, in the case of the Rodents, the masticating surface of their incisor teeth has no enamel. According to Owen (34), the pharyngeal teeth of Labrus are composed of ordinary dentine alone. Amongst Fishes, as, for example, in the Pike, a common arrangement is the combination of a central mass of vascular dentine (vasodentine, Owen), with a thin cap of ordinary dentine, which in the most external layers is homogeneous, and very hard (vitro-dentine, Owen, 34). Compare fig. 120.

DENTINE (Substantia Eburnea, Ebur).—Dentine forms a yellowish-white, highly elastic, but friable mass, presenting a finely fibrous, peculiarly lustrous fracture, and is one of the hardest constituents of the animal body. Its chief components are a very firm matrix, analogous to compact bony tis-

Fig. 119.

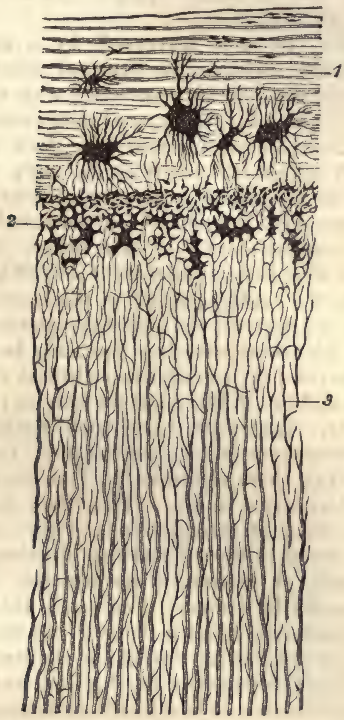

Fig. 119. Canine tooth of Man, presenting a portion of the transverse section of the root. 1. Cement with large lacunæ and parallel striæ. 2. Interglobular substance. 3. Dentinal tubules. Magnified 300 diameters.

sue, and extremely fine, frequently branched fibres—the *dentinal fibres* of Tomes (40) and Kölliker (58), which occupy fine canals, the *dentinal canals* traversing the matrix. The dentinal fibres are enormously elongated processes of the so-called dentinal cells, or cells of the dentinal pulp (*odontoblasts*). Dentine consequently corresponds to bone, with this difference, that instead of cells it contains the long processes of cells in its calcified matrix. In regard to the other characters of the matrix, it presents a similar uniformity of appearance, and a similar chemical composition, to that

of compact bone. After treatment with acids (especially with dilute hydrochloric acid) a material, *dentinal cartilage*, is obtained which is precisely similar to ossein, except that it is of somewhat firmer consistence.

The dentinal fibres constitute the soft parts of dentine. They do not lie in direct contact with the hard matrix, but are invested by sheaths, the *dentinal sheaths* of E. Neumann (48), which are intimately connected with the matrix. After the fibres have been removed by maceration, or by incineration of the tooth, the dentinal sheaths remain, and even after destruction of the matrix by boiling in strong muriatic acid or in caustic alkalies, they constitute the only perfectly indestructible residue of the tooth. They form the white finely fibrous felt which still remains after treatment with the above-mentioned reagents. The dentinal sheaths, it is highly probable, belong to the category of elastic limiting layers which not unfrequently form around the cavities of the connective tissues. E. Neumann considers them to be calcified (see also p. 101).

The dentinal matrix, then, is traversed by a number of fine canals, having walls of a peculiar nature—the dentinal sheaths—in which lie the dentinal fibres. The *dentinal canals* commence with small circular openings on the inner surface of the pulp cavity, and pass radially outwards through the dentine, making numerous spiral turns in their course (Welcker, 41). As a general rule each tubule extends from the pulp cavity to the enamel, or cement, giving off in its course numerous delicate transverse branches. By means of these transverse branches both the tubules and their contents —the dentinal fibres—anastomose with each other. In sections made from fresh teeth, examined with high powers (500—1,000), it is not difficult to recognize, especially in the central section of the course of the tubules, which is of considerably larger diameter, the pale homogeneous dentinal fibre. The lining of the tubules (dentinal sheaths) can only be satisfactorily seen in cross section, when they appear as delicate yellowish rings, in the interior of which the transverse section of the dentinal fibre is perceptible in the form of a minute dark point. I, at least, agree with Kölliker (58) in this interpretation of the appearances seen on cross section. Carious teeth prove very serviceable in exhibiting these relations.* The dentinal tubules are best examined in fine sections dried in air. They then make their appearance, filled with air, in the form of strongly defined very dark tubules or lines, enabling them to be traced to their finest ramifications.

In regard to the mode of peripheric termination of the dentinal tubuli no positive conclusion can be drawn. Yet exact information on this point is of considerable importance, because Tomes (29) has directed attention to the sensibility of the peripheric portion of the dentine.

Wherever the terminal loops occur the dentinal tubuli must also end in the same manner; nevertheless, it is difficult to demonstrate actual terminal loop-like structures. Extremely fine processes of the dentinal tubuli run towards the enamel, and are lost at the surface of the dentine. At this part also larger or smaller irregularly defined cavities are found, *the interglobular spaces* of Czermak (33), which will be more fully considered hereafter. The dentinal tubuli open into these interglobular spaces, and from them again fine processes extend towards the enamel. A direct passage of the dentinal tubuli into the enamel does not occur.

Tomes (29) and Kölliker (58) are strongly of opinion that some of the dentinal tu-

* In the vicinity of carious portions of tooth, both the soft dentinal fibres and the dentinal sheaths are thickened, so that in transverse sections both come very clearly into view.

buli, with their soft contents, penetrate into the enamel. This they think especially occurs amongst the Rodents and Marsupials. I have not, however, been more successful than Hertz (52) in convincing myself of this fact. No conclusion can be drawn with positive certainty from sections, since the slightest deviation from parallelism in the surfaces may easily produce deceptive appearances. So, again, fissures in the enamel, and inequalities of the adjacent surfaces of the dentine and enamel, might easily lead to the view supported by Tomes. The question can only be determined by the examination of young teeth in process of development; but I have never been able to discover anything of the kind. Intervening between the dentine and the cement is a considerable quantity of the already mentioned interglobular substance, and the greater number of the dentinal tubuli open into its irregular spaces. These again are continuous with the lacunæ of the cement by means of fine canaliculi. The tubuli may be followed quite to the free surface of the masticatory surface of the incisor teeth of the Rodents, where the dentine is freely exposed; but it appears to me that in the peripheral portions of these tubules the dentinal fibres are atrophied.

If we now proceed to consider the *dentinal fibres* with more minuteness, no further reference to their course and direction is needed, since these are determined by that of the tubules, which have already been sufficiently described. At the same time it is not easy to decide whether the fibres are present in the finest peripheric ramifications of the tubules. In young teeth this is certainly the case, but in those that are older, atrophy of the fibres appears to be concurrent with obliteration of the canaliculi. We may seek in vain, even in young dentinal fibres, for rudiments of nuclei, although both the history of their development and several pathological appearances (as for instance those accompanying caries) might lead us to expect their presence. The fibres easily stain with carmine. They possess a remarkable degree of extensibility, so that, especially in young teeth, the dentinal cells may be separated to a considerable distance from the dentine without rupture of the processes, which then appear like harp strings stretched across the interval. Salter (51), in recently describing the fibres as tubules, because, when dry, they appear to contain air vesicles, and exhibit a dark central point on section, has probably had the dentinal sheaths under observation. The fibres are really completely solid and homogeneous.

There are some remarkable deviations from the above-described structure of the dentine. The *interglobular substance* is in the first place a structure tolerably widely distributed. Czermak has described under this name those parts of the dentine which, when thin sections are dried in air, appear beset with irregular spaces and cavities. The walls of these spaces, especially if they form a deep notch, often project in the form of spheroidal masses or dentinal globules. Indications of a spherical form which sometimes occur in the compact dentine are explicable on the supposition that the interglobular spaces have been obliterated by calcification of their soft contents, the contours of their original walls being to some extent retained. The contents of the interglobular spaces consist of a soft mass. In the young fresh teeth of the calf, rounded and stellate cells may frequently be seen in the larger interglobular spaces, with processes which extend into the dentinal canals opening into them. At a later period the cells atrophy, or their protoplasm becomes converted into a substance analogous to the dentinal cartilage. In immediate proximity to the cement, a layer of very small, closely compressed interglobular spaces is very constantly present, forming the *granular layer* of Tomes. The interglobular spaces, with their soft contents, are therefore only the result of a somewhat irregular process of dentinification, and are analogous to the small irregular medullary cavities found in the interior of compact bone.

In the dentine of many animals, especially of Fishes, of some Rodents, in the central portion of the tusks of the Elephant, the molar teeth of the Iguanodon and others, vascular canals exist analogous to the Haversian canals of bone, constituting the *vaso-dentine* of Owen. In Man this form of dentine is only met with as a consequence of the secondary ossification of the pulp. In many Fishes (Kölliker, 45) the

bones of the skeleton consist in great part of true dentine; whilst conversely we find in the dentine of the teeth, especially in pathological conditions, masses with bone lacunæ, termed Odontomes by Virchow, and Osteo-odontomes by Hohl, which occur in the dentine near the cement, or in ossifications of the pulp, and form the *osteo-dentine* of Owen.

Transitional forms, between vaso-dentine, osteo-dentine, and ordinary dentine, are frequently met with in Fishes, as, for instance, in the Pike. In the Cetacea, Dugong, and Physeter, again, the peripheric layer of the dentine, which contains a large number of small interglobular spaces and true bone corpuscles, passes without interruption into the investing cement, so that it is impossible to draw here any definite line between osseous substance and dentine.

Schreger (7) first recognized a system of concentric lines running parallel to the contour of the teeth in dentine, which in large teeth can be easily seen with the naked eye, or with a low magnifying power. In true dentine they present on section a characteristically decussating course with small rhomboidal meshes between them. As Retzius (19) and Owen (25) first correctly stated, the lines of Schreger are occasioned by the corresponding primary curvatures of the dentinal tubes. Owen (25) describes in addition a second system of parallel curved lines in dentine, the *contour lines* occurring especially in the tusks of the elephant, produced by regularly intercalated strata of small cells (probably finely granular interglobular substance). Czermak and Kölliker give similar illustrations, drawn from the teeth of man; we are not however justified from these appearances in concluding that dentine possesses a lamellated structure.

Fig. 120.

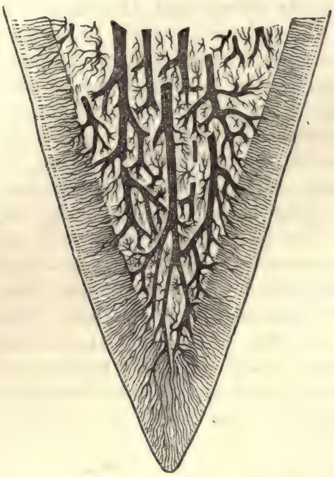

Fig. 120. Apex of a tooth from the lower jaw of the Pike (Esox lucius). Magnified 80 diameters. The central portion consists of vaso-dentine, which is covered with true dentine; external to which again is a thin layer of vitro-dentine.

ENAMEL (Substantia Vitrea; Subst. Adamantina; Encaustum; Adamas; Email).—Enamel is the hardest substance met with in the Vertebrata, being in this respect about equal to Apatite (F. Hoppe-Seyler, 69). With its translucent mass and bluish tint it forms a kind of cap of various thickness, investing the crown of the tooth, usually following its contours with accuracy. Its surface, especially at the sides, exhibits very fine, nearly parallel, transverse striæ (Czermak), which are probably referrible to the papillary structure of the *enamel organ* (see this). Coarser projections

with deep grooves, which have likewise been described by Czermak, must be regarded as pathological formations.

In young teeth, examined at that stage in which the enamel is still soft and capable of being cut with a knife, it is easy to demonstrate that it consists of rather elongated prisms of about 3—5 μ long, which are called *enamel fibres*, or *enamel prisms* (see fig. 124, 4 and 5). It is impossible to avoid perceiving a certain similarity in form between these and very long columnar epithelial cells, like those which form the fibres of the lens. This is especially obvious in fine transverse sections, which exhibit a delicate mosaic with six-sided areas. After cautious treatment with dilute hydrochloric acid and subsequent boiling in $S\,O_3$ (Beigel (50), whose method otherwise affords no special advantage), the enamel prisms can be easily isolated in adults. Their extremities are often pointed like a needle, which, however, appears to depend only on irregular fracture. By the same means, also, it can be shown that the prisms partly run in a straight direction, and partly in curves; but I have not been able to satisfy myself that angular or zigzag curvatures occur, as stated by Czermak. The dark transverse striæ and slight varicosities which, especially after the addition of very dilute hydrochloric acid, occur at regular distances from one another in the isolated prisms of enamel, are very remarkable. If the treatment with hydrochloric acid be continued for some time longer, the fibres split in the direction of the clear transverse lines into small cubic fragments of nearly equal size (3—4 μ).

It still remains a question how the transverse bands are to be explained. The circumstance that they are generally absent, or at least are not so well marked in young soft fibres, and that their relative thickness nearly corresponds to the thickness of the fibres, has led me (49) to express the opinion that they might proceed from the decussation of the fibres. I am well aware of the grounds adduced by Hertz (52) against this supposition, and which are assented to by Kölliker; but I must still consider it doubtful whether all enamel prisms exhibit transverse striæ and varicosities. Hertz returns to the intermittent (schubweise) calcification of the enamel cells formerly admitted by Hannover (39). But the mode in which so regular a transverse striation is thus produced, is, to me at least, unintelligible; besides, no evidence can be brought forward showing that a laminated mode of formation occurs in enamel.

The enamel fibres lie in close contact with each other, without any demonstrable intervening substance. They appear to be completely solid, and extend for the most part through the whole thickness of the enamel. At the same time they pursue a very various course, which finds its expression in the well-known *decussation* of the prisms. We accordingly find that alternate layers of enamel fibres appear on section to run vertically and transversely, in consequence of which a peculiar and sometimes very regular pattern is produced. The enamel prisms must therefore also pursue, in the form of fasciculi, a various and often decussating course towards the surface of the tooth. A second pattern presenting itself in the enamel is formed by the so-called *brown parallel striæ* of Retzius, which are superimposed lines coursing in the same direction, and regarded by Kölliker as the expression of a laminated mode of formation of the enamel.

These are frequently (see fig. 118) very fine, and closely applied to one another; some appearing to be more conspicuous than others. No satisfactory explanation of this phenomenon can at present be given. Hertz attributes it to deposits of pigment in the enamel prisms, as occurs, for example, in the beaver and squirrel, where it is due, according to V. Bibra (68), to the presence of oxide of iron; and in these Rodents, according to Wenzel (66), such deposits are already present in the protoplasm of the enamel cells; still, no positive statements can at present be made on this point. Other

kinds of striæ, again, may be perceived on examining transverse sections, and most distinctly after brushing with dilute hydrochloric acid (1 : 12, Hertz), which are caused, according to Czermak, by the regular zigzag course, or, according to Hannover, by twisting or spiral turns of the prisms. An explanation will be hereafter given of the decussation of the prisms, as well as of their various course (see the Development of the Enamel). The observations of Hoppe-Seyler (69) on the behavior of the enamel in polarized light are replete with interest. According to these, fully developed enamel exhibits strongly negative double refraction, and is probably uniaxial; whilst young enamel presents positive double refraction. Adult enamel becomes positive on being exposed to a temperature of 800° C. Hoppe-Seyler (69), in one of his analyses, found the composition of the enamel of the newly born infant to be PO_5 3 Ca O O=75 23, C O_2, Ca O=7·18, Cl Ca=0·23, PO_5 3 Mg O=1·72. Organic compounds=15·59. The enamel of adults contains only from one to three per cent. of organic constituents; but, on the other hand, a large quantity of phosphate of lime. A remarkable feature is the presence of a small proportion of fluorine.

THE CUTICULA (*persistent capsule* of Nasmyth, 22; schmelzoberhäutchen of Kölliker) forms an extremely resistant investment not more than 1—2 μ in thickness, covering the exposed portion of the teeth, and disappearing wholly when they are mature. When the enamel is present, the under surface frequently presents the impression of prisms in the form of small square areas.

Kölliker and others more recently have improperly applied the term enamel membrane to the cuticula, since it is developed with equal distinctness in teeth in which the enamel is absent, as for instance in the Pike.]

In young teeth, examined when in the act of perforating the gum, the cuticula may be easily detached as a whole after slight action of hydrochloric acid. It may then be tinted with solution of nitrate of silver, which causes the appearance of figures similar to large epithelial cells. These, as the history of the development of the teeth shows (see this), are the cornified cells of the so-called external epithelium of the enamel organ, from which the cuticula is formed.

The chemical relations of the cuticula dentis indicate that it belongs to the category of horny substances. According to the statements of Kölliker (58), which I am able to corroborate, boiling water and mineral acids exert no action upon it, except that it is stained of a yellow color by nitric acid. When boiled with caustic potash or soda, it softens, and when burnt yields a smell resembling that of horn. I have not been able to prove the presence of lime in the cuticle of man; small traces of this substance could always be referred to imperfect purification of the membrane from enamel or dentine in contact with it; so that it is questionable whether it undergoes any calcification. Kollmann (67a) has recently admitted this, but offers no proof.

CEMENT (Zahn-kitt, *osteoid substance*, *cementum*, *cortex osseus*, *crusta fibrosa*).—The cement is a true bony structure essentially belonging to the periosteum of the alveolus, and in man and many of the vertebrates forms a thin investment to the fangs of the teeth. Intimately connected with the dentine, it commences as a delicate covering at the neck of the tooth, where the enamel ceases, and is thickest at the apices of the roots and in the depressions between the roots of the molar and bicuspid teeth. In the folded enamel and compound teeth the cement penetrates deeply in the form of a moderately thick layer between the projections of the crown, or serves as a connecting substance to the several toothlets; it is therefore situated for the most part external to all the other constituents of the tooth. The Pachy-

dermata and others have also a special covering of cement, investing the whole crown of the tooth as a secondary formation (crown cement).

Both in its chemical and microscopical characters, cement is closely allied to bone. The lacunæ are for the most part large, and possess an enormous number of very long canaliculi, especially in the Cetacea. When the cement is extremely thin, however, they may be entirely absent, and it then presents on section a perfectly homogeneous and vitreous appearance. A similarly very hard lamella, destitute of lacunæ, occurs also in the outermost portion of the thicker layers of cement. Haversian canals, which sometimes open into the pulp cavity (Salter, 58), are found when the cement is thick, though it is rare to find any lamellated arrangement of the matrix.

Kölliker (58) has described peculiar cavities in the cement, which he considers to result from pathological processes. Sharpey's fibres also occur, and I have found the cement of the dog to be that best adapted to show them. The thick capsule-like investments surrounding one or several lacunæ, first noticed by Gerber (24) in the cement of the horse, are deserving of especial mention. These lacunæ, with their thick capsules, can be easily isolated in diluted acids, and may be regarded as nests of osteoblasts formed in the process of ossification, and surrounded by thick sheaths of connective tissue.

Soft Structures of the Teeth.—The soft tissues belonging to the teeth include *the tooth pulp and the gums.* The former is the vascular and nervous matrix of the dentine, and the remains of the original tooth papilla. It constitutes also the model of the tooth on which the hard structures are formed like a cast, and therefore presents, in accordance with their difference in shape, an extremely various form. In old teeth, where the hard parts predominate to a remarkable extent, there remains only an inconsiderable residue of the pulp enclosing the cavum dentis, and in the human tooth it is reduced to a very slender thread containing a few vessels and nerves. The pulp is immediately connected with the periosteum and base of the alveolus by means of the foramina dentium.

In the incisors of the Rodents, which produce new dentine continuously, the pulp, even in adults, retains its original character, and its structure can there be best studied.

The principal portion of a good specimen of young pulp consists of indistinct finely fibrous connective tissue containing numerous cells, that recalls in many respects the mucous tissue of old atrophied umbilical cords, the elastic tissue only being absent. On account of the numerous large vessels which break up immediately beneath the surface into a plexus of capillaries of moderate width, the tissue appears quite cavernous. The external layer of the pulp is formed by a layer of large cells, of elongated form, and provided with numerous processes, called *Odontoblasts* (49, 59), which are arranged so as to form a kind of columnar epithelium.* These cells (see figs. 123, 124) are from 20 to 30 μ on the average in length, and about 5 μ in breadth. They are finely granular, and destitute of a membrane. The moderately large rounded or ovoid nucleus is usually contained in that end which is turned towards the pulp. In adults, as Boll (59) remarks, the form of the cells is very slender, whilst in young teeth they are more or less compressed. Three kinds of processes may be distinguished in these cells. The dentinal process, the pulp process, and the lateral processes.

* The names formerly applied to them were dentinal cells (Elfenbeinzellen). Kölliker terms this entire layer of cells membrana eboris, because after the pulp has been withdrawn it usually cleaves to the inner surface of the tooth in the form of a continuous membrane-like layer.

The dentinal processes constitute the above-described dentine fibres; it need here only be repeated that from one cell several dentine fibres are frequently given off (Boll counted as many as six). Such odontoblasts, with several dentinal processes, are broad at the end, directed towards the dentine, but as the processes pass on they gradually diminish to form dentinal fibres. The odontoblasts are intimately connected with each other by means of the fine short teeth which the lateral processes of all dentinal cells form. The short pulp process usually springs from the cell with a moderately broad base, and is constantly connected with one of the cells lying immediately beneath the membrana eboris, which last are usually somewhat larger and more darkly granular than those more deeply seated.

We are indebted to Boll (59) for first furnishing us with precise information in regard to the nerves of the teeth. He observed in the incisor teeth of the Rodents, after the pulp had been macerated for an hour in a solution of chromic acid containing $\frac{1}{32}$ per cent., a very large number of non-medullated extremely fine nerve fibres, which exhibited a silky lustre, and were gradually but directly continuous with the medullated fibres. If the observer is so fortunate as to preserve the membrana eboris in its natural connection with the pulp, which Boll sometimes accomplished by introducing a fine knife between the pulp and the dentine, after treatment with chromic acid, the extraordinary richness of these non-medullated fibres in the peripheric portions of the pulp becomes apparent. Preparations that have been teased out with needles show that the nerve fibres pass outwards between the odontoblasts in considerable numbers, and accompany the dentinal processes to which they are subjacent in the form of fine hairs. Boll was, however, unable to see the actual penetration of the nerve fibres into the dentinal tubuli, although their length and the direction they pursued rendered this probable.

The *gum* is distinguished from the other portions of the oral cavity by its vascularity and its large papillæ, which again, like the papillæ fungiformes, are beset with small projections (Kölliker, 58). No glands appear to be present in them. Here and there small round heaps of pavement epithelium, frequently presenting the appearance of concentric lamellæ of horn, are met with, either imbedded in the substance of the gum, or occupying fossæ on its surface (Serres, 8; Kölliker, 58). The periosteum of the alveoli, which fulfils the office of periosteum, not only to the internal surface of the alveolus, but also to the cement, termed the Periodontium, is characterized by its softness. It contains but few elastic fibres, though I, with Kölliker (58), have found its nervous supply abundant.

Dentinal structures occur in large numbers, and present a great variety of form, amongst the Invertebrata. The teeth of the masticatory apparatus of the Echinus most closely resemble those of the Vertebrata. H. Meyer * states that they are composed of enamel fibres; this, however, is not quite accurate. The teeth of the Echinidæ are long, slender, slightly curved plates, which present a well-marked longitudinal ridge on their inner surface. The greater part of each tooth is formed by a radial lamina attached vertically to the surface of this ridge or keel. The radial lamina is moderately soft, and can be easily broken up into thin leaflets, which are again composed of elongated prisms somewhat curved at their extremities. The peripheric plate is considerably harder, and its prisms are much smaller and softer than those of the keel. Between these prisms, which in part run parallel to one another, and partly decussate in each plate, lie thin lustrous calcareous plates which often exhibit an extremely delicate plexus of fine anastomosing canaliculi. When treated with hydrochloric acid, the prisms dissolve with the disengagement of a large quantity of gas, and leave no organic residue. They appear, therefore, to be entirely composed of carbonate of lime. In their degree of hardness, in their size and chemical characters, they consequently differ remarkably from true enamel, and they do not possess the regular four or six-sided form, characteristic of the fibres of the latter substance. In Mollusks,

* Müller's *Archiv*, 1849, p. 191, *et seq.*

Worms, and Arthropods the oral or gastric teeth are composed of chitine, which is sometimes impregnated with lime or silica. It may be said generally that the teeth amongst the Invertebrata are to be regarded as pure mineral or epithelial structures (and are therefore analogous to the enamel), whilst in the lower Vertebrata they are chiefly composed of peculiarly modified and ossified connective tissue; in the higher classes of animals, which present the most complicated form of dentinal structures, an epithelial structure (the enamel) is again included in their structure.

Development of the Teeth.—The genesis of the teeth in the human embryo commences, according to the observations of Robin and Magitot (46), at about the fiftieth to the sixty-fifth day. The margins of the jaw, at the beginning of the third month, form a slightly raised rounded ridge, the "*maxillary ridge*," which is most prominent in the lower jaw, and consists of a thickening of the embryonic connective tissue and epithelium of the mucous membrane of the mouth. This epithelium, with its vascular substratum resembling mucous tissue, constitutes therefore the matrix of the several constituents of the teeth, the *epithelium forming the enamel*, and the *mucous tissue the dentine and cement.*

The "*enamel organ*" is formed by a peculiar structure resulting from the growth and multiplication of the epithelial cells, which dip down into the mucous tissue. In a direction contrary to this there is then developed a papilliform process of the mucous tissue, the origin of the pulp and of the dentine. The two parts together constitute the rudiment of the tooth.

Fig. 121.

Fig. 121. Upper jaw of a fœtal sheep three centimetres in length. Vertical section, magnified 50 diameters, showing the enamel germ, with the semi-lunar rudiment of the dentine germ and dental sac in transverse section. 1. Dentinal groove. 2. Palatal process.

When at a later period the connection of the enamel organ with the oral epithelium is interrupted, the rudiment of the tooth is enclosed in the alveolar border of the jaw on all sides, as in a capsule, by the sub-epithelial connective tissue. That portion of the connective tissue which immediately invests the rudiment of the tooth is usually termed the "*dental sac*," and at a later period forms the *cement.**

Enamel Organ and Enamel.—Near the end of the second month of fœtal

* Kölliker (58) calls the entire rudiment of the tooth enamel organ, papilla dentis, and the connective tissue investment of both, "dental sacculus," and distinguishes the latter again as "proper dental sacculus," a nomenclature which has little to recommend it.

life the margin of the jaw exhibits a slight longitudinal furrow, with rounded borders, termed the "dental groove." The epithelium of the oral cavity completely covers it, so that it is scarcely perceptible when the surface alone is examined. The two projecting borders of the groove are termed the "dental ridges" (Marcusen, 31), or "lips of the dental groove" (Dursy, 67). Soon, from the bottom of the dental groove, a narrow process of the oral epithelium dips into the subjacent mucous tissue, presenting on section the form of a short tubular gland, but in point of fact constituting an epithelial fold along the whole length of the jaw—the *enamel germ* of Kölliker (47). The primary dental groove, especially of the upper jaw, increases in size, and becomes entirely filled with oral epithelium. The epithelium also becomes extraordinarily increased in thickness on the two dental ridges, and in the deep groove between the lips and the margin of the jaw, especially in Ruminants (Kölliker, 47). At some points the enamel germ appears to descend perpendicularly from the base of the furrow into the subjacent tissue, but in other regions, especially in the neighborhood of the incisors, it extends obliquely towards the median line, and consequently forms a larger or smaller angle with the dental groove.

Fig. 122.

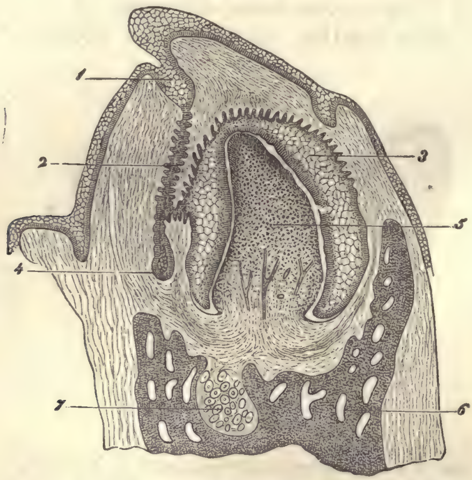

Fig. 122. Vertical section of the inferior maxilla of a human fœtus, measuring eleven centimetres from the vertex to the coccyx. Magnified 25 diameters. 1. Dental groove. 2. Remains of the enamel germ. 3. Enamel organ presenting externally epithelium, as also where it forms the enamel germ of the papillæ of the dental sacculus. 4. Secondary enamel germ; rudiment of the permanent tooth. 5. Dental germ. 6. Lower jaw. 7. Meckel's cartilage.

The above account differs from that which I formerly gave, in recognizing a *dental groove* in the vicinity of the subsequently appearing dental rudiment, and in not regarding this groove as a secondary formation caused by an hypertrophy of the epithelium. Kölliker (58) also describes a groove of this nature, and figures it with the enamel germ proceeding from its deepest part.* The statements of Marcusen (31) on the development of the teeth, which I have already indicated as being the first that were accurate (49), require still to be followed out in further detail. Dursy (67) has very recently entered minutely into the description of the first occurrence of

* *Loc. cit.*, fig. 260.

the dental groove, and has accompanied his statements with numerous illustrations. He considers it to be formed by an inequality in the growth of the margin of the jaw. He regards the enamel germ as resulting from the progressive development of the dental furrow and its epithelium, which, however, does not penetrate more deeply into the margin of the jaw, but is rendered deeper by the increased elevation of the margins. I believe, however, that we must draw a distinction between the small primary dental groove with its epithelium and the true enamel germ. The latter is a secondary formation which, although proceeding from the epithelium of the primary dental groove, is yet distinguished from this, both by its sudden attenuation, by the difference in its direction, especially in the case of the incisor teeth, and by its microscopic characters. The epithelium of the dental groove, with the exception of the deepest layer, consists of large spherical or flattened transparent cells. The cells of the deepest layer are columnar, and are immediately continuous with the similarly formed cells situated at the periphery of the enamel germ, whilst the cells at the centre of the enamel germ are dark, granular, and round. Even at a later period we must still distinguish between the continuously enlarging dental groove and the enamel germ (see fig. 122.) Whether the enamel germ penetrates by its own growth into the blastema of the jaw, as I have described (49), or becomes more deeply imbedded in consequence of an increase in height of the dental walls, it will perhaps be difficult to decide. The small primary dental groove superjacent to this, which is not always present, may however be identified with the dental groove of Arnold (12) and the primitive dental groove of Goodsir. Both overlooked the enamel germ, and imagined the teeth to be developed from isolated papillæ in their dental groove.

A series of remarkable changes soon take place in the more deeply seated portions of the enamel germ, especially at the several circumscribed spots corresponding to the later developed milk teeth. The spheroidal cells forming the central part of the enamel germ begin to increase with rapidity, so that the germ becomes conically elongated, assuming the form of a club, which is continuous by means of a relatively narrow neck with the epithelial cone of the dental groove. Coincidently the dentine germ increases in a contrary direction, forming a club-shaped mass, and projects upwards into its base, so that the enamel germ comes to invest the dental papilla like a cap. The connection between the several portions of the enamel germ then become dissolved, probably in consequence of an increase of the connective tissue of the dental ridges, so that now a special division of the enamel germ, which since the time of Purkyné (14) has been *called the enamel organ*, corresponds to each of the dentinal germs. Each enamel organ is thus composed of a strongly developed portion that surmounts the dentine germ like a cap, and a narrow cord of cells extending to the epithelium of the mouth —*the neck of the enamel organ*, which represents the remains of the primitive enamel germ (see fig. 122). The neck of the enamel organ disappears at a later period, whilst the two dental ridges coalesce with one another above. The rudiments of the teeth are thus surrounded on all sides by the loose connective tissue of the wall of the jaw.

Histological changes of a very remarkable character occur in the enamel organ, coincidently with the morphological changes that have been described above. The marginal cylindrical cells, where they are in immediate contact with the dentine, appearing as an epithelium covering it, become remarkably elongated, and form very regular six-sided prismatic bodies—in fact, the most beautiful and regular columnar epithelium found in any part of the animal body (see figs. 123 and 124). The sides of the cells present a distinct limiting membrane; but the protoplasm has no investment at the two extremities. At the base of the dentine germ, where it becomes continuous with the lateral walls of the enamel club, the cells become progressively shorter, until at last they assume a cubical form, and thus coat the portion of the internal surface of the enamel organ, or rather of the dental sacculus, which is turned away from the dentine germ. In accordance with

Kölliker (47), we designate the elongated cylinder cells as the *internal* or *enamel epithelium*, and the remaining marginal cells as the *external epithelium* of the enamel organ. As far as the external epithelium reaches, the adjoining connective tissue exhibits tolerably regularly formed conical and vascular papillæ, which project into the epithelium, and correspond to the papillæ found in the remaining portions of the oral mucous membrane (see fig. 122).

The complete continuity and concatenation of all these structures is most satisfactorily proved by a recent statement made by Dursy (67), which I am able to corroborate, that especially towards the neck of the enamel germ, similar papillary structures are present, which here pass without interruption into the papillæ of the gum. It is only requisite to remark that they are much stronger, and developed at an earlier period, in the enamel organ than in the gum.

Fig. 123.

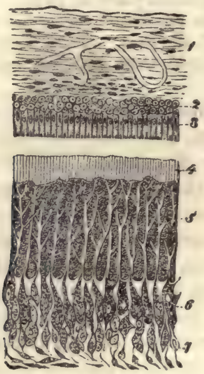

Fig. 123. Longitudinal section of a milk tooth from the fœtal sheep, carried through the margin of the dentine pulp and adjoining portion of the enamel organ. Magnified 200 diameters. 1. Dental sacculus. 2. External epithelium and stratum intermedium here united to the internal epithelium or enamel cells 3. after the disappearance of the enamel pulp. 4. Young layer of enamel detached from the enamel cells. 5. Dentine. 6. Odontoblasts. 7. Part of the dentine pulp.

The small round cells of the enamel organ between the external and internal epithelium undergo at the same time a peculiar transformation. They acquire a stellate form, and unite with each other by their processes in the same manner as the cells of ordinary mucous tissue, which this part of the enamel organ so strikingly resembles that up to the time of Huxley (37) and Kölliker (47) they were always regarded as gelatinous connective tissue. The cells, however, lying in immediate contact with the epithelium (stratum intermedium of Hannover, 39) retain their original form, and from these a continuous development of enamel cells, as well as of gelatinous epithelial tissue, appears to proceed. The enamel cells may be frequently seen to be in connection at their lower extremities with the cells of the stratum intermedium, so that a multiplication of the enamel cells from the cells of this stratum in the direction of their length may be admitted to occur (see fig. 124, 2). The jelly of the enamel organ (enamel pulp) possesses only a transitory and mechanical significance, occupying the space subsequently required by the growing tooth. Nevertheless, before the

formation of the enamel is completed, both the epithelial and gelatinous tissue and the stratum intermedium undergo atrophy. The outer and inner epithelia consequently again come into close apposition (see fig. 123); the latter is entirely used up in the formation of the enamel, and in teeth examined just at the period of eruption we can only detach from the enamel a membrane composed of one or more layers of very flat epithelial cells, which clearly represent the outer epithelium with a larger or smaller amount of the stratum intermedium. As soon as the eruption of the tooth is effected, these cells become horny, and form the cuticula dentis.

Fig. 124.

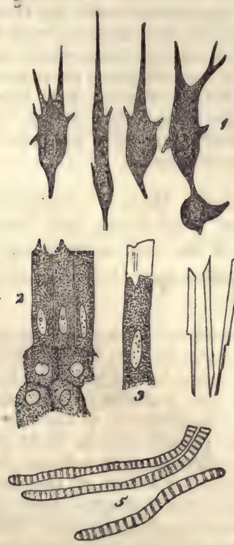

Fig. 124. Highly magnified. 1. Various forms of odontoblasts. 2. Three enamel cells, with a few cells of the stratum intermedium attached; two enamel cells exhibit Tomes' processes. 3. An enamel cell, with a small portion of enamel. 4. Fragments of enamel fibres from young and still soft enamel (acicula). 5. Old enamel fibres with transverse striæ.

This conversion, so remarkable in a histological point of view, of a portion of the epithelial cells of the enamel organ into stellate gelatinous tissue, finds an analogy, according to Kölliker (58), only in the cells of the external investment of the egg of the Perch. I have myself occasionally met with a similar metamorphosis of the epithelial cells in the Graffian follicles, but never occurring in so regular a manner. Renewed investigations, notwithstanding the objections raised by Kölliker (58) and Kollmann (67 a), compel me to adhere to the view I have above expressed of the nature of the cuticula dentis. Its tenuity cannot be considered as an objection, especially if, as I am now inclined to believe with Hertz (52), the external epithelium is alone to be regarded as the basis of the cuticula.

The formation of the enamel is purely and exclusively referrible to the enamel epithelium, the enamel prisms resulting from the *direct calcification* of the long cylindrical cells. The intimate connection of enamel cells with small portions of the enamel prisms, which remain adherent to the cells in the form of processes, is in the first place in favor of this view (see fig. 124, 3). Again, the limit to which the calcification extends is not bounded by a straight

line, but is very irregular, a circumstance that is opposed to the idea of a calcification of any secretion formed by the enamel cells. If young enamel be treated with diluted acids, the enamel prisms swell up to some extent, and reassume the form of the original columnar cells, and the distinct membranous investment of the longer sides comes into view. The disappearance of the nucleus in such calcifications and metamorphoses of cells is so common, that there is nothing remarkable in its absence in those of the enamel.

Kölliker (58) has recently so far inclined towards the view propounded above, that he appears inclined to explain the formation of enamel in the same sense as Schwann (23), who held that the enamel cells continued to grow at their free extremities, and that the new growth underwent continuous calcification. Hertz (52) and myself (49) transfer the growth of the cells to the nucleated extremity directed towards the stratum intermedium, which is more in accordance with the facts observed, and with the general mode of increase of cells; for the nucleus, with the immediately surrounding protoplasm, is always that part of the cell from which the phenomena of life radiate with the greatest activity, whilst the peripheric portions constantly, on the other hand, have a tendency to death or to transformation into intercellular substance, etc. In favor of the same view also is the remarkable circumstance, that in all elongated columnar cells, with one nucleus in their interior, the latter is constantly found to occupy the attached and never the free extremity.

From the foregoing remarks, then, it appears that enamel is to be regarded as the *petrified dental epithelium*, and that its essential part corresponds to the mucous layer of the oral epithelium, whilst the cuticle, though perhaps by a secondary metamorphosis, is associated with the horny structures.

The delicate membrane described by Huxley (37), in his account of the structure of the teeth, which can be raised with tolerable facility from the surface of the developing enamel after it has been subjected to the action of hydrochloric acid, is the youngest layer of the enamel as yet but slightly impregnated with mineral constituents (Tomes, 29). The foraminated appearance of the membrane is in favor of this view. The enamel cells first undergo petrifaction in their investing (external) zone, the axial portion of the protoplasm retaining its softness for a time, and in isolated cells forming a kind of process (Tomes' Process of the Enamel Cells (49), see fig. 124, No. 2). As a consequence of this the youngest layer of enamel must necessarily exhibit a number of foramina, corresponding to the "Processes" of Tomes. Huxley correctly identifies this membrane with the *membrana præformativa* of Raschkow, but erroneously considers the cuticula dentis to proceed from it. Raschkow described a thin homogeneous membrane investing the dentine germ, which was regarded by Todd and Bowman, and by Kölliker, as a basement membrane of the dental papilla covering the surface invested by epithelium (enamel cells). Huxley (37) and Kölliker also describe a basement membrane between the mucous membrane and the external epithelium. Such a membrane is, however, only discoverable when the enamel cells have attained a certain stage of development, and have already begun to be calcified. If this membrane, which exhibits the characteristic foramina of Huxley's membrane, be raised by the action of hydrochloric acid, no other homogeneous basement membrane can be demonstrated on the dentine germ.

The papillary projections of the dental sacculus directed towards the enamel organ afford an explanation of many of the peculiarities in the course of the enamel fibres which have been mentioned above. In the first place, the fine transverse striæ which run in a circular direction around the external surface of the enamel are directly referrible to the papillæ. For if, towards the end of the formation of the enamel, the enamel pulp disappears, and the external and internal epithelial cells again come into contact with each other, the papillary processes make their mark on the enamel membrane, and naturally also on the product of its calcification, the enamel. The transverse elevations of the latter are thus of precisely the same nature as the well-known fine striæ of the nails. Moreover, since the greater part of the enamel is formed before the enamel jelly has disappeared, and therefore at a time when the enamel membrane already exhibits the impressions of the papillæ, we may reasonably refer many peculiarities in the course of the enamel prisms, especially their decussations, spiral course, and undulations, as well as their optical characteristics, to the same cause.

Dentine and Cement.—As Dursy (67) maintained, the first germ of the dentine appears in the dental sacculus as a dark semi-lunar area at the bottom of the dental groove—that is to say, of the enamel germ—coetaneously and continuously with which it is developed along each half of the jaw (see fig. 121). At certain points corresponding to the position of the subsequent teeth the young structure develops in the form of papillæ projecting against the enamel germ, whilst the remainder atrophies. The two horns of the semi-lunar mass (seen in section) extend, from the base of the dental papilla, some distance upwards, and embrace the dentine germ and the enamel organ. This constitutes the first trace of the *dental sacculus*, which at this period consists of tissue somewhat richer in cells and vessels than the mucous tissue of the dental groove. The dental sacculi are only well defined at the earlier periods of the formation of the tooth. When the process of development is more advanced, it is impossible any longer to distinguish a capsule-like layer of connective tissue around it. Moreover the dentine germ is only a special division of the mucous tissue of the dental groove, unusually rich in vessels and cells. After it has attained a certain size, the *odontoblasts* above described develop from the cells lying at the periphery, and we soon recognize a solid shell of dentinal bone superimposed on the dentine germ, like a cap. The histological formation of the dentine is precisely similar to the ordinary process of ossification.

Whilst the peripheric portions of the odontoblasts constantly undergo metamorphosis, with disappearance of their nuclei, into a gelatigenous matrix which subsequently undergoes calcification, their centric portions penetrate the hardened mass in the form of longer or shorter threads, and represent the first rudiments of the dental fibres. The lateral processes of the odontoblasts occasion the numerous anastomoses of the dental fibres, or of the dental tubuli. Every odontoblast communicates with the more deeply situated and successively enlarging cells of the young pulp by means of its pulp process, so that when an odontoblast is calcified up to the base of the fibre, another occurs in its place without any interruption to the continuity of the fibre. Hence every dental fibre, with its anastomoses, must be regarded as formed of several continuous odontoblasts. The layers of matrix immediately surrounding the fibres undergo conversion, as appears from their chemical characters, into elastic tissue, and form the dental sheaths of Neumann. It has not yet been ascertained whether they also undergo calcification. *Thus it appears that the dentine, with all its constituents, proceeds from odontoblasts that have become metamorphosed in their form and chemical composition.*

No further detail respecting the process of dentinification need here be entered upon, since, so far as regards the osteoblasts, it presents the most complete analogy to that of ossification (see p. 108).

This analogy is still more close in regard to the formation of the cement, in which the histological processes are identical with those of intra-membranous ossification. The matrix of the cement is the loose myxomatous connective tissue of the dental alveoli which immediately surrounds the teeth, and so far we may thus consider the dental sacculus to be the matrix of the cement. A special cement germ, such as has been described by Robin and Magitot (46), in certain species of animals, as in the Ruminants, Pachydermata, etc., does not, according to my observations, exist.

In animals with successive teeth, as Kölliker (47) has demonstrated, a process is found, even at the period of the first appearance of the enamel organ at its median side, which is either given off from the neck of the

enamel germ or from a still deeper part, and becomes the enamel organ of the persistent teeth (see fig. 122). On the other hand, no trace of a dentine germ for these latter teeth is at this period visible.

Hertz (52) mentions the occurrence in several preparations of a second inflection of the oral epithelium superjacent to the enamel germ of the milk teeth, which he is inclined to regard as the enamel germ of the persistent teeth. Nevertheless there is much here that requires elucidation, especially in respect to the formation of the three molars of man, which, as is well known, are not preceded by milk teeth.

The processes occurring in second dentition have been very recently minutely investigated by Kehrer (56) and Lieberkühn (57). As the persistent tooth projects, the alveolar wall dividing it from the milk tooth sacculus undergoes absorption, and with this there immediately occurs a process of cell proliferation in the sacculus of the milk tooth, under the influence of which the fang, with the formation of the so-called Howship's lacunæ, is absorbed as far as the crown. The young granulations in the mean while take the place of the fang of the milk tooth. The remains of the pulp of the milk tooth unite with the granulations now causing erosion, which, however, are themselves compressed by the growing tooth, that pushes the remains of the milk tooth so far forward that it falls out. No obliteration of the vessels of the milk tooth occurs. The true mode in which absorption is effected, the formation of the lacunæ of Howship, is no better understood here than in the case of the absorption of bone. Kehrer believes, from finding chalk granules in the protoplasm of young cells, that the amœboid cells of the granulations destroy the dental tissue by a kind of mining process, effected by their pseudopodia.

The Gubernaculum of the second set of teeth, already described by the older anatomists, consists, according to the observations of Lieberkühn, only of a cord of connective tissue, which traverses the alveolus in order to conduct the nerves and bloodvessels to the dental sacculus. It has no relation to the process of dentition itself.

Our knowledge of the development of simple teeth consisting only of cement, dentine, and probably also always of cuticle, requires revision. According to the statements of Owen (25), these neither possess an enamel organ, nor form a closed dental sacculus.* We possess no accurate information of the relations of the oral epithelium. Probably there is here, as Leydig (36) describes in several species, as, for example, in the Anguis fragilis, a thin covering to the freely projecting dental papilla, which subsequently becomes the horny cuticle. In accordance with a more recent investigation of Leydig (62), the crowns of the teeth, which, however, have no investing enamel, originate in Salamandra maculosa, in several dental sacculi which lie at the bottom of the "epithelium of the jaw." The fangs are developed from the subjacent connective tissue. Leydig considers the substance of the dental crowns to be a cuticular formation.

The simple horny teeth do not differ in their formation from the ordinary papillæ of the oral mucous membrane possessing a strong horny investment. Nothing is at present known of the mode of development of the more compound forms occurring in Ornithorhyncus and others.

Accurate knowledge of the dental tissues, and of their development, commences with the works of Purkyné and his scholars, Fränkel (13) and Raschkow (14). Leeuwenhoek (2) had indeed previously seen the dental canaliculi, and, like J. Hunter (4), had recognized the cement as a distinct substance, the discovery of which is ordinarily attributed to Blake (5) and Tenon (6); still it is only from the time of Purkyné that the knowledge of this subject has become common property. The enamel fibres have been

* Owen, moreover, claims enamel for many animals, in which it does too exist, as, for instance, the frog.

described by many from the time of Malpighi. Retzius (19) and Hannover (39) gave the most accurate description of the structure of the dentine and enamel, especially with regard to the various lines and markings upon and in them, and the course of the canaliculi and enamel fibres. Nasmyth (22) and Erdl (27) first described the cuticle, and Czermak (33) the interglobular substance. We are indebted to E. Neumann (48) for the demonstration of the dental sheaths, and to F. Boll (59) for following out the dental nerves in their further course. In recent times, Tomes (29, 40) has most successfully worked at the finer points of dental structure, and by demonstrating the dental fibres first opened the way to a correct interpretation of the nature of the dentine; previously to him, as by J. Müller (16) and Lessing (28), the dental canaliculi were regarded in reference to their contents precisely in the same light as the lacunæ of bone. Tomes also furnished numerous and valuable contributions to the comparative anatomy of the teeth. On the latter subject, however, the important work of Owen (25) constitutes the principal authority, but those of Erdl, Hannover, Huxley (37), Agassiz (15), F. Müller, and Henle (20) may also be enumerated. Amongst the points in the histology of the teeth still requiring elucidation the structure of the enamel and the final terminations of the dental nerves deserve to be mentioned. If we except the works of Arnold (12) and Goodsir (21) (who, however, considered that the teeth originate from free papillæ at the bottom of an open dental groove) as constituting the first comprehensive investigations towards the elucidation of the genesis of these structures, those of Marcusen (31), Huxley (37), and Kölliker (47, 58), have proved of the highest value. Marcusen gave the minute details of the primary origin of the teeth quite correctly, and referred the enamel to the oral epithelium, as Huxley also has always maintained; and Kölliker's accurate investigations have placed the fact beyond doubt. Purkyné and Raschkow had already demonstrated the enamel organ, Schwann (23) the enamel cells and odontoblasts, and Lent (38) and Kölliker (58) the dentinal processes of the latter. The external epithelium has likewise been correctly described and explained by Marcusen. All later observers, Nasmyth, Huxley, Natalis, Guillot (44), Todd and Bowman (35), Robin and Magitot (46), notwithstanding that they described this epithelium with great minuteness, have furnished us with no new information respecting it. Dursy (67) has followed the papillary processes of the dental sacculus, together with the intervening depressions of the external epithelium which frequently appear as glandular structures belonging to the latter, as far as the enamel germ, and from thence on to the papillæ of the maxillary mucous membrane. To judge from his description and illustrations, Hérissant (3) must have already seen the papillæ, which he considered to be glands for the secretion of enamel. Their importance in the formation of enamel has not been sufficiently estimated. Most of the contested points await their elucidation from an accurate knowledge of the histogenesis of the dentine and of the enamel. Kölliker (58), with whom Hertz (52) is in accordance, so far as regards the dentine, and Kollmann (67a), in regard to the enamel, still considers both substances as a hardened excretion of the odontoblasts or enamel cells; whilst Tomes, Hertz, and Wenzel (66) (in the continuously growing incisors of Rodents), in regard to the enamel, and Boll recently in regard to the dentine, agree with a view given in the text. Kollmann admits also a membranous investment to the free ends of the enamel cells; this continuous layer forms the membrana præformativa, and at a later period, when calcified, the cuticula dentis.

In the following account of the literature of the subject, besides the most

recent works, only those are mentioned which have given either extended and complete descriptions, or have furnished some new facts. References to the older literature are well given in Hérissant, Henle (26) and Robin, and Magitot.

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CHAPTER XVI.

THE INTESTINAL CANAL.*

By E. KLEIN AND E. VERSON.

A. Oral Cavity, by E. Klein.

The mucous membrane of the oral cavity in man begins at the lips as a direct continuation of the outer integument.

Three anatomically different parts† can be distinguished in it: a cutaneous, a transitional, and a muco-membranous portion.

The transitional portion is marked off from the cutaneous portion by the outer border of the red lips, and from the muco-membranous portion by the most prominent part of the convexity of the lips, so that when the mouth is closed the red visible portion of the lips represents the transitional portion.

The cutaneous portion is covered by a thin epidermis consisting of one or two layers of flattened epithelium intimately fused with one another; subjacent to this is a thinner mucous layer, in which are small rounded cells containing relatively large nuclei.

The cutis internal to this is composed of fasciculi of fibres, which decussate with one another, the principal ones being directed towards the free border of the lips. The fibres which form these fasciculi consist, for the most part, of fine connective tissue fibres, between which isolated or plexiform fibres of elastic tissue run.

The surface of the cutis directed towards the epidermis presents rows of cylindrical or conical small vascular papillæ standing in tolerably close proximity with one another, and projecting into the rete mucosum to about half its thickness. The nervous and vascular trunks proceeding from the subcutaneous tissue, or from the muco-membranous and transitional portions, make their way between the muscular fasciculi, and curve at nearly right angles in the cutis. Hairs and sebaceous follicles are distributed in moderate number at nearly equal distances, and at various depths in the tissue. The hair follicles of the upper lip are directed obliquely downwards at their base, those of the lower lip upwards. The points of distinction between the transitional and the cutaneous portions of the lips are the absence of hair follicles and sebaceous glands in the former; the presence of wedge-like fasciculi of the orbicularis oris in it, which reach nearly to the epithelium; the much greater transparency of its superficial cells; the arrangement of its morphological elements generally; and, lastly, its far more abundant supply of blood-vessels.

The epithelium, as a whole, remains at a short distance from the last hair follicles, as deep as at the cutaneous portion, but beyond this rapidly

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* The account given in this section rests on investigations which the authors have undertaken in my laboratory for this work.—S. Stricker.

† E. Klein, *Zur Kenntniss des Baues der Mundlippen des neugebornen Kindes*, "On the Structure of the Oral Lips of the newly born Child;" *Sitzungsberichte der k. k. Akadem. der Wissenschaften in Wien*, December Heft, 1868.

increases in thickness. The superficial cells are much flattened, intimately fused with one another, and without apparent nuclei; but those which are rather deeper, though still tabular, become somewhat elongated, and possess a well-defined and usually elongated nucleus. The cells of the middle layers increase as they are more deeply situated in their vertical diameter, and become proportionately narrower, with round nuclei; the deepest cells are round, with relatively large spheroidal or irregularly shaped nuclei.

The chief fibrous layer of this transitional portion is composed of broad highly refractile fibres, capable of resisting the action of acetic acid, and united into plexiform fasciculi. The fasciculi separate from each other at many points to permit the passage of the horizontally coursing vascular trunks, which are here very numerous.

The thickness of this layer is least where the hair follicles cease; from this point it gradually increases, and is thickest at the commencement of the muco-membranous portion. Its surface is beset with very numerous thin and elongated papillæ, which are frequently clavate, oblique in direction, and vascular.

Between the fibrous layer and the submucous tissue of the muco-membranous portion, and near the commencement of the latter, are situated the coronary artery and vein. These give off larger and smaller branches to form a plexus beneath the epithelium from which the vessels for the supply of the papillæ arise.

The third part of the lip, the muco-membranous portion, possesses an epithelium that far exceeds in thickness that of the two above-named portions; but if this be followed over the fold of the lip, it will be found again quickly to diminish. It presents the several layers characteristic of laminated flattened epithelium; the most superficial layers consisting of flattened tubular cells, with a flattened and for the most part elongated, though occasionally spheroidal, nucleus; subjacent to these are cells that at first are of greater breadth than depth, but become in the deeper layers more and more polyhedric, till they are finally succeeded in the deepest layers by cells which are arranged in the form of palisades.

Many of these cells are ribbed, or exhibit thorn-like projections, by virtue of which they are connected with each other by a dentated suture.

The tissue of the mucous layer is composed of finer and coarser fibres. The former are either united into fasciculi, or run, in the form of fine isolated or paired elastic fibres, sinuously between or in many spiral coils around the decussating and plexiform fasciculi. Besides these, broad, highly refractile, strongly looped fibres occur.

Wherever the fibres of the membrana mucosa pursue any definite general direction, it is horizontal, and directed from one side of the lip to the other. Moreover, numerous fasciculi pierce the muscular layers to reach the subcutaneous tissue of the transitional portion. Near the muscular fasciculi the tissue undergoes alteration, becoming less dense, and the mucous membrane passes into submucous tissue.

The membrana mucosa is beset with conical, usually undivided, but occasionally bifid or trifid papillæ, which often, coming into contact at their wide bases, project into the epithelium; the longest of these (0·525—0·63 of a millimetre in length) are situated at the commencement of the muco-membranous portion posteriorly; coincidently with the diminution in the thickness of the epithelium they likewise become shorter, and do not exceed half the depth of the epithelium.

The epithelial cells covering the papillæ are arranged in an imbricated manner, and are much flatter than the cells situated on the same level between

the papillæ. Corresponding to the first two or three rows of papillæ situated at the commencement of the muco-membranous portion, the epithelial surface presents a small elevation; and in newly born children the papillæ of this part of the lip, and those at the angles of the mouth, project as much as one millimetre beyond the lower plane of the epithelium.

The glands that are situated in the submucous tissue of the muco-membranous portion make their first appearance behind the most prominent portion of the convexity of the lip, and, indeed, at that point where the epithelium begins to be constant in thickness.

They constitute acinous glands that are essentially similar to the salivary glands. Our knowledge, however, is not sufficiently advanced to enable us to state that they present those characteristics of the salivary glands which have been the subject of recent investigation. They open on the surface of the mucous membrane or epithelium by means of small excretory ducts. Each of these is a canal bounded by a structureless membrane, in which the laminæ of tesselated epithelium only extend to the depth of the epithelial layer generally; beyond this it is lined by a single layer of cylindrical epithelium. After pursuing a spiral course obliquely through the membrana mucosa it gives off numerous branches, which frequently divide and terminate in the individual acini. The acini belonging to a large branch are united into a lobule by the fasciculi of the submucous connective tissue, and these again are formed into lobes. The fasciculi and fibres which limit a lobulus or a lobe, and in the meshes of which the several acini are imbedded, are continued as a sheath to the excretory duct in its passage through the mucous membrane. The plexiform tissue composed of fasciculi of fine connective tissue fibres belonging to the submucous layer, and which, together with delicate frequently coiled elastic fibres, forms the framework of the gland, is at the same time the support of small nerves, and of a close system of capillaries which surround the acini.

In this tissue there lie, partly isolated amongst the fine fibres of the connective tissue fasciculi, partly accumulated in larger numbers near and around the acini, lymph corpuscle-like cells, as well as large, coarsely granular, irregularly shaped masses of protoplasm, which usually contain a small nucleus.

Sebastian * counted fifty-seven glands in the lower lip alone; in other cases there were thirteen and twenty-one of these glands. Their diameter amounts from ½ to 1½ millimetre, or more; and as a rule their size increases in proportion to the smallness of their numbers; they are largest in children, and diminish as age advances.

In the lower lip of the child † they are arranged in four or five consecutive rows. Their number rarely exceeds three in the upper lip, and they are altogether absent at the angles of the mouth.‡ I find that in the child they are larger in the lower than in the upper lip. Besides the glands, large vessels and nerves are also found in the submucous tissue of the muco-membranous portion, the latter for the most part running in a vertical direction, giving off smaller branches to the mucous membrane, which again subdivide, and may be followed to the immediate vicinity of the epithelium.

The nerves of the papillæ have not been accurately investigated. According to

* Sebastian, *Recherches anatomiques, physiologiques, pathologiques, et semeiologiques sur les Glands Labiales.* Gröningen und Bremen, 1842, 4to.

† E. Klein, *loc. cit.*

‡ Henle, *Splanchnologie*, p. 138.

W. Krause, the so-called terminal bulbs—structures respecting the nature of which there is still some doubt—are found in the lips of many Mammals.*

Kölliker † has observed in the papillæ of the lips, but only of that part which is visible when the mouth is closed, tactile corpuscles, and in one instance he found nerve coils in the small papillæ, and at the bases of the larger. Gerlach ‡ also ascribes tactile corpuscles to the papillæ of the borders of the lips.

The fasciculi of the musculus sphincter oris are intercalated between the submucous tissue of the muco-membranous portion and the subcutaneous tissue of the cutaneous portion. According to C. Langer,§ the muscular fibres of each side have three points from which they radiate towards the median line, namely, the angle of the mouth, and the two musculi incisivi; from the angles of the mouth the fibres arranged in a laminated manner pass to the lips, one portion terminating without crossing the median line in the cutis of its own side, another passing beyond this to terminate in the skin of the lip on the other side, and, finally, a portion of the fibres attaching themselves to the incisor processes of the bones on the same side. Moreover, according to Langer, the fibres of the sphincter penetrating the cutis lose themselves amongst its plexiform fibres. Woodham Webb ‖ has likewise, some time ago, demonstrated the presence of transversely striated muscles in the lips of Man, from which extremely delicate fasciculi extend into the papillæ of the cutis, and are there lost. It may be shown by carefully made sections that a portion of the muscular fibres which Langer and Woodham Webb considered to penetrate the cutis belongs to a peculiar system of muscular fibres (compressor labii) which arise in the spaces intervening between the first 5—7 consecutive rows of hair follicles, arrange themselves in the subcutaneous tissue in four or five fasciculi, traverse, forming slight curves, the fasciculi of the sphincter, and at their entrance into the muco-membranous portion, that is to say, into the submucous layer of this portion, every two or three fasciculi decussate alternately, in order finally to penetrate the mucous membrane itself in a fan-like manner, or, more rarely, to enter its transitional portion.

The several muscular fibres, both of the muco-membranous portion as well as of the cuticular portion, may be followed into close proximity with the epithelium, or to the base of the papillæ. The sarcolemma is continued for a short distance between the fibres of the membrana mucosa, or of the cutis, in the form of delicate fibres. In the cutaneous portions the muscular fibres partially decussate at the base of a hair follicle, whilst elsewhere they may be followed on the wall of the hair follicle to near the rete mucosum.

This muscle in the lower lip is more strongly developed near the middle line than at the sides; but in the upper lip, in which it is usually more feebly marked, the opposite obtains. Laterally the fibres are directed radially towards the oral opening, and the area embraced by its origin and insertion is larger.

At the angles of the mouth the mucous membrane rests upon the inner surface of the buccinator, and extends, as the mucous membrane of the

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* W. Krause, *Die terminalen Körperchen.* Hannover, 1860.

† *Zeitschrift für wissenschaftliche Zoologie*, Band iv., Heft i. p. 43.

‡ *Handbuch der allgemeinen und speciellen Gewebelehre des menschlichen Körpers. Mainz*, 2. Aufl.

§ *Ueber den Musculus orbicularis oris, Wiener Medicinische Jahrbücher*, Heft ii.; *und Zeitschrift der Gesellschaft der Aerzte.* Wien, 1861.

‖ "On Striated Muscular Fibres in the Skin of the Human Lip," *Quarterly Journal of Medical Science.* London, 1857, January, Vol. v., p. 89, plate vii., fig. 16.

cheeks, as far back as to the anterior border of the vertical ramus of the lower jaw, without presenting any important variation in its structure. Its epithelium is of the same thickness and structure as that already described as covering the muco-membranous portion, except that the number of ribbed cells in the middle layers of the mucous membrane of the cheeks is much greater than that of the lips.

The form of the papillæ which project from the Memb. mucosa into the epithelium is irregular; they are often conical, with elongated apices, or with their points prolonged in a filiform manner. At their bases they are relatively broad. Their height varies, sometimes amounting to half the depth of the epithelium, sometimes scarcely exceeding its lower boundary line. The Memb. mucosa is most dense beneath the epithelium, and in it the same arrangement of the elements may be recognized as in that of the lips. Towards the buccinator muscle it becomes more loose. Its fasciculi stand in the same connection with those of the subcutaneous tissue as in the case of the lips.

The glands of the mucous membrane of the cheeks (Glandulæ buccales) are thinly scattered, and are only to be found at considerable distances from each other; near the point where Steno's duct opens they also form a series of glands known as the glandulæ molares.* According to Ward, they are from two to four in number, are situated between the masseter and buccinator muscles, and are larger and composed of more lobules than the remaining glands of the oral mucous membrane.

At the point where the lips are reflected upon the anterior surface of the jaws, the mucous membrane at the middle line, both above and below, forms a small duplicature, termed the *frænum.*

The epithelium of the mucous membrane is here thinner than elsewhere; the papillæ are also smaller and less numerous; the mucosa itself is not distinguishable. The vessels are relatively numerous, and it contains a considerable number of fine irregularly coursing elastic fibres.

That portion of the mucous membrane which covers the alveolar processes of the jaw, and surrounds the necks of the teeth, passing anteriorly into the mucous membrane of the lips, posteriorly at the root of the oral cavity into that of the hard palate, and below into that of the floor of the mouth, is named the *gum* (Gingiva).

The *gum*, on account of the abundance of tendinous fasciculi it contains, is denser and tougher than the mucous membrane of any other part of the mouth; it is intimately adherent to the bone in consequence of the direct prolongation of the tendinous fasciculi of the periosteum into the mucosa.

The epithelium of the gum is composed of laminæ of tesselated cells, amongst which are exceedingly well-marked ribbed cells. The superficial cells are strongly flattened; those more deeply situated become thicker, and possess strongly defined ribs. The deepest cells are cylindrical, with conical external extremities.

The *papillæ of the mucosa* of the gum are all relatively broad at their bases, of unequal height, with conical or rounded external extremities, which are sometimes simple and sometimes divided.

The tissue of the mucosa is tough, and is composed of broad fasciculi of connective tissue, the fibres of which run in a straight direction. It also contains a not inconsiderable number of finer or coarser closely coiled fibres. In the mucous membrane of the gum, three separate fibrous layers may be distinguished: *a.* Fasciculi of fibres which run in a horizontal direction

* N. Ward, art. "Salivary Glands," in Todd's *Cyclopædia of Anatomy and Physiology*, Vol. ii., p. 422.

from right to left parallel to the surface, and then break up into smaller fasciculi that, after frequently decussating, reunite into coarser bundles; these predominate on the anterior surface of the alveolar process over the two following sets of fibres. *b.* Fasciculi which, proceeding from the periosteum of the alveolus, cohere in large bundles, and immediately again break up in a fan-like manner, whilst coursing towards the epithelium, either from before backwards or from behind forwards. On approximating the epithelium, the smaller fasciculi break up into isolated fibres, which, running apparently between the cells, penetrate the deepest epithelial layers. *c.* Lastly, there are fasciculi which run in a vertical direction from above downwards, or from below upwards, and in other respects resemble those described under *a.*

At the posterior part of the gum of the upper jaw, where this passes into the mucous membrane of the hard palate, all three sets of fibres frquently decussate.

The nerves of the mucous layer of the gum are not numerous.

The mucous membrane of the *hard palate* presents many differences in structure from that of the gum. The laminated pavement epithelium, which at first is thinner than that on the gum, gradually increases in depth posteriorly. The number of ribbed cells contained in its middle layers varies at different points. The papillæ of the mucous membrane projecting into the epithelium are not nearly so numerous at the commencement of the hard palate as on the gums. The median papillæ, especially near the foramen incisivum, are frequently observed, through tracts of considerable extent, to be indicated only by sparingly distributed slight depressions of the deep surface of the epithelium. Posteriorly the papillæ increase somewhat in number and height, although even in some parts of the posterior third of the hard palate they are not much larger than quite anteriorly.

The mucous layer subjacent to the epithelium is thinnest over the anterior third of the median line; more externally it is generally thicker, attaining its maximum posteriorly.

The fasciculi, as a general rule, run as if they radiated from the arch of the alveolus of the upper jaw towards the median line of the hard palate. In the anterior part of the mucous membrane, consequently, they run from before backwards, but more posteriorly from side to side.

Their constituent elements consist anteriorly, for the most part, of broad fibres, which form a close plexus beneath the epithelium; but at a plane somewhat deeper there is a loose network of connective tissue, constituting a submucous layer, the fibres of which are more densely matted as they approach the bone, and finally become continuous with the periosteum. In the middle and posterior thirds the mucous membrane beneath the epithelium is looser in texture, but at a deeper level the fasciculi of connective tissue are woven into a compact felt, and separate in the submucous tissue from one another to form meshes of variable size. Laterally the submucous tissue contains fat cells which are most abundant in the middle third.

The vessels and nerves run in the submucous tissue of the middle line and lateral portions of the anterior third, the former pursuing for the most part a longitudinal, the latter a transverse direction. The more externally the part examined is situated, the more numerous are the nerves, the small branches of which form arches in the mucosa. In the middle part of the hard palate, and in the first instance laterally, acinous glands occur in the submucous tissue, which are isolated in front, but subsequently grouped either into a single or (towards the posterior and external portion of the

middle third) into two longitudinal rows. Szontagh counted 250 glands in the hard palate.*

After the mucous membrane of the oral cavity has covered the hard palate, it forms posteriorly a muscular fold, the *velum palati*, or soft palate, which presents in man a conical median prolongation, the *uvula*, and is also continuous with the mucous membrane of the nasal passages. The mucous membrane of the soft palate is continued laterally and downwards as the arcus palato-glossus into that of the root of the tongue, and as the arcus palato-pharyngeus into that of the pharynx.

In newly born children the apex of the uvula and the immediately adjoining parts are covered with tesselated epithelium, whilst the posterior or upper surface is invested with a laminated cylindrical and ciliated epithelium. The most superficial cells are here beset with short hair-like processes, present a conical form, with the apices directed away from the surface, and contain rounded or laterally flattened nuclei; subjacent to these are fusiform or elongated oval cells, and still deeper lie others that are flattened at the sides by mutual pressure.

The transition of laminated pavement epithelium into laminated cylindrical and ciliated epithelium is effected by a diminution in the number of the middle layers of the cells, which are not arranged as before, with their shortest diameter perpendicular, but parallel to the surface; and by the disappearance of the most superficial flattened cells, which are replaced by cylinder cells, that increase in number in proportion to their distance from the apex of the uvula.

On the posterior surface of the uvula and of the soft palate of the newborn infant there may moreover be found numerous isolated areas, presenting well-developed pavement epithelium, as well as transitional forms between the laminated cylinder and pavement epithelium. In adults † a laminated pavement epithelium exists both on the anterior and on the posterior or superior surfaces of the uvula and soft palate, and this may be divided into two layers, of which the cells forming the deeper are smaller than those of the superficial.

The tissue of the mucous membrane contains fasciculi of connective tissue, and a considerable quantity of coiled elastic fibres of various size united into plexuses. The part situated immediately beneath the epithelium, is much closer in texture than that which is deeper, and forms the submucous tissue in which the glands and muscles are found. The fasciculi of connective tissue found in the velum palati and uvula may be considered to run in three directions: the first of these, for the most part lying externally, run horizontally and from side to side; the second longitudinally; and these two sets form the felt of the mucosa; lastly, there is a third set, which, emanating from the first two, runs from the mucosa in an obliquely divergent manner into the deeper parts, in order to enter the mucosa of the opposite side. These last-mentioned fibres form, by their decussation, the loose network of the submucous tissue of the soft palate and uvula, which, as usual, contains a variable quantity of fine elastic fibres, small lymph corpuscles, and large connective tissue corpuscles, with numerous vessels and nerves. In the soft palate and uvula of the adult there project from the

* Szontagh, *Beiträge zur feineren Anatomie des menschlichen Gaumens*, "Essays on the Minute Anatomy of the Hard Palate in Man;" *Sitzungsberichte der k. k. Akademie der Wissenschaft. zu Wien.* März Heft, 1866.

† E. Klein, *Ueber das Epithel des Weichen Gaumes*, etc., "On the Epithelium of the Soft Palate," etc.; *Wiener Sitzungsberichte der k. k. Akademie der Wissenschaft. zu Wien*, Jänuar Heft, 1868.

surface of the mucous membrane into the epithelial layer conical or cylindrical papillæ with rounded extremities. These papillæ are much larger and more numerous on the uvula than on the soft palate. (In one transverse section of the uvula of an adult I counted 130 in a single plane.)

In the velum palati of the new-born infant the relations of these parts are somewhat different. In such I find no papillæ on the upper surface, but the vessels advance as far as the epithelium, and there loop back, or course for some distance immediately beneath the epithelium. On the inferior surface again we find similarly looped vessels forming broad and flat arcades, especially in longitudinal sections, immediately subjacent to the deeper surface of the epithelium, or a bloodvessel with a little mucous tissue may project into the inferior layer of the epithelial cells. These appearances may be remarkably well seen at the borders of the folds. Two or three branches may there be seen to be given off from a larger vessel, and, accompanied by a little fibrous tissue, to penetrate between the epithelial cells. At the most prominent portion of the folds two or three pointed papillæ appear of equal breadth but variable length. The mucous membrane of the velum palati is extraordinarily rich in vessels. Just beneath the epithelium, as well as in the deeper layers of the mucosa, besides numerous extremely thin-walled bloodvessels, there are numerous lymph channels, both in the form of larger lymphatic lacunæ and of lymphatic vessels. The larger nerve trunks lying externally to the first rows of glands, the number of which is much more considerable at the anterior than at the posterior surface, give off fine branches, which run both internally into the submucous tissue as well as externally into the mucosa, where they may be followed in the former instance between the glands and the muscles, in the latter as far as the epithelium.

The thickness of the mucosa is variable, and depends on the size and number of the glands. In general the thickness of the mucous membrane increases from the commencement of the hard palate towards the point of the uvula, and it is always somewhat thicker on the upper surface than on the lower.

The acinous mucous glands of the soft palate are situated, as has been noted above, in the submucous tissue. Their size varies, and the largest are found in the uvula. Szontagh * counted one hundred of them on the anterior surface of the soft palate, forty on the posterior surface, and twelve on the uvula. In the last-named situation they become larger, and form in its upper half, or basis, a central layer, which, however, is somewhat nearer to the anterior surface than to the posterior, and is sometimes invested by the fasciculi of the azygos uvulæ, and at others is intercalated between the two muscles.

The excretory ducts vary in their width, in the nature of their coats, and in their direction. At the posterior surface of the uvula in adults we find excretory ducts which become wider near their orifice; but the opposite obtains in the ducts opening on the upper and lower surfaces of the soft palate. The direction pursued by the excretory ducts is very rarely rectilinear; the greater number, after they have received all their tributary branches, run from the deepest part of the mucosa perpendicularly towards the epithelium, then turn off at an angle, and course obliquely towards the free surface of the epithelium. They are for the most part lined with a simple cylindrical epithelium; in other instances, but less frequently, beneath the cylindrical cells a second layer of small round cells is found, and

* *Loc. cit.*

at the posterior surface of the soft palate the excretory ducts of a few glands exhibit, even in the adult, for a short distance from the epithelial surface, a lining of ciliated cylindrical cells.* The laminated pavement epithelium of the surface may in some cases be followed for a short distance as a lining to the excretory ducts of the glands.

Fig. 125.

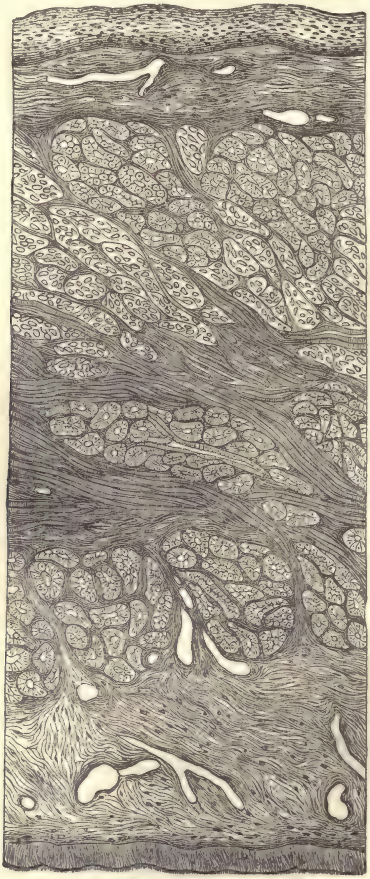

Fig. 125. Longitudinal section of the soft palate of a Child. *a a*, ciliated epithelium; *b b*, mucous membrane of the upper surface; *c*, glands; *d d*, muscular fibres of the thyreo-palatinus; *e e*, muscular fibres of the levator palati; *f*, mucous membrane of the lower surface; *g*, epithelium of the lower surface.

The course and arrangement of the muscles in the soft palate are highly complicated. The only true longitudinal muscle contained in it is the azygos uvulæ, or palato-staphylinus, a double muscle, the two portions of which arise at the fibrous border of the hard palate, and are situated on either side of the median line. In the anterior part of the soft palate the two portions

* E. Klein, *loc. cit.*

are distant from each other about their own diameter,* but near the base of the uvula they are in close proximity. They do not quite extend to the apex, but terminate at about the end of the second third, the fasciculi becoming fan-shaped anteriorly, and expanding to the greatest extent at the sides, consequently corresponding in their course, and terminating in the same mode as has been described in speaking of the muscles of the lips. In their passage through the soft palate, several small fasciculi are given off from the principal mass, which, traversing the lobules of the glands, and surrounding them, rejoin it, or dip into the mucous membrane, especially at its anterior surface, and terminate in the mode described.

The Musculus thyreo-pharyngo-palatinus † constitutes the chief muscular mass of the soft palate. It is divisible, according to Luschka, into a thyreo-palatine and a pharyngo-palatine portion. The upper extremity of the former lies partly in front of and partly behind the Levatores, decussating with them to some extent. The greater number of the fibres of the pars thyreo-palatina lie in front of the Levatores, and form a curved flattened muscle, with a maximum breadth of nine millimetres, which is situated nearer to the hard palate than the arch formed by the junction of the two Levatores by about the breadth of this arch. The convex border of this portion is continuous with the fibrous border of the hard palate or aponeurosis of the tensor veli palati, whilst its concave border is turned towards the similar concave border of the arch formed by the Levatores.

The other fibres of the upper extremity of this pars thyreo-palatina, situated behind the Levatores, form in the adult several loosely connected fasciculi, much interrupted by fat cells, which, becoming more and more delicate towards the free border of the soft palate, course partly in front of the azygos uvulæ between the glands of the anterior surface, and partly over or behind it between the glands of the posterior surface, either ending here or extending to the mucous membrane. The thyreo-palatine portion of the muscle just described receives reinforcing fibres from the Levatores ; ‡ and a fasciculus is constantly given off laterally from these where they unite to form an arch, which, subdividing, runs in front of the azygos to the opposite side, and there joins the innermost bundles of the pars thyreo-palatina. The whole of these fibres run outwards and downwards, descending with the arcus pharyngo-palatinus, and are partly inserted in the upper angle of the thyroid cartilage, and are partly united with the pars pharyngo-palatina, forming the posterior wall of the pharynx. The pars pharyngo-palatina arises near the arcuate extremity of the pars thyreo-palatina, and the two unite together in the arcus pharyngo-palatinus, and pass to the posterior wall of the pharynx. Besides what has been already stated respecting the Levatores veli palati, it still remains to be observed that the arcuate junction of these two muscles is situated in front of the azygos uvulæ, and in the anterior half of the soft palate.

Finally, there is a small muscular fasciculus which arises from the transverse fibres of the tongue, and runs in the anterior arcus glosso-palatinus towards the base of the uvula, where it is partly lost in the mucous membrane of its anterior surface, and partly unites with the ultimate bundles of the thyreo-palatinus.

The several fasciculi of the palatal muscles, like those of the tongue and lips, form a delicate plexus. A considerable quantity of adipose tissue

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* Szontagh, *loc. cit.*

† Luschka, *Der Musculus pharyngo-palatinus des Menschen*, Virchow's *Archiv*, Band xlii., p. 480.

‡ Luschka, *loc. cit.*, p. 483.

generally enters into the structure of the palate in adults, being chiefly found between the fasciculi of the thyreo-palatinus and the levator palati. It also constantly occurs between the first layer of glands of the upper surface, and is to be met with, in larger or smaller quantity, in various parts of the mucous membrane.

The muscular folds of the mucous membrane which extend as the arcus glosso-palatinus and pharyngo-palatinus, from the soft palate to the root of the tongue and pharyngeal wall, exhibit no peculiarity of structure differing from that of the mucous membrane of the soft palate; the epithelium, papillæ, and muco-membranous tissue being in all essential respects similar. Elastic tissue, forming plexuses, is usually abundant in the mucous membrane of these folds. The lowermost glands diminish in number and size in adults, present the same dimensions as those of the uvula, and are united into a layer, the continuity of which is interrupted by a sparing amount of loose connective tissue containing fat cells surrounding the lobules and acini, and here and there by small muscular fasciculi. The tissue of the mucous membrane is frequently infiltrated at the free border of the folds with a greater or less number of lymph corpuscles. These infiltrated portions, in which may be recognized, besides numerous bloodvessels, a delicate cellular network with decussating fibres of connective tissue, are never sharply defined, but pass gradually into the adjoining tissue.

Between the palatine arches the lateral walls of this part of the oral cavity, known as the Isthmus faucium, present a depression; from the bottom projects a swelling—the tonsil, which is sometimes so small in newly born children as to be scarcely perceptible on inspection of the oral cavity from before, and is sometimes so large that the two organs materially contract the dimensions of the isthmus. Their surface is lobulated by fissures of various depths and complexity. The whole organ is to be regarded as a thickened portion of the mucous membrane, presenting a lobulated surface, the proper membrana mucosa of which constitutes a kind of conglobate gland substance (Henle), consisting partly of fibrous, and partly of adenoid tissue, in the meshes of which numerous lymph corpuscles are contained. The epithelium is here tesselated and laminated; papillæ can scarcely be said to be present. Beneath the epithelium is a close plexus of vessels, and the infiltrated mucosa is divided into portions resembling Peyer's patches by means of connective tissue cords proceeding from the submucous tissue. Acinous glands are distributed in the submucous tissue, and they are in contact externally with the muscular tissue of the pharynx.

The Tongue.

That surface of the tongue in Man which is directed towards the palate—dorsum of the tongue—presents different characters from the lower surface; for in the former the papillary elevations of the mucosa covered with tesselated epithelium project to a considerable extent, and confer upon it its peculiar furred appearance; whilst on the lower surface the papillæ of the mucous membrane do not in general project more than to half the thickness of the epithelium. The surface of the descending portion of the tongue in the newly born child, again, presents different features from that of the adult; in the former, the surface of the mucous membrane appears tumefied, the swellings being divided by elongated fissures; in adults, on the other hand, it is beset in many places with numerous smaller and larger lenticular elevations, which sometimes possess a small opening. The mucous membrane on the lower surface of the tongue, when in the contracted condition, exhibits numerous

fine parallel folds like those which, under all circumstances, are to be found upon the sides, posterior to the level of the foramen cæcum.

The papillæ freely projecting from the surface of the tongue are termed, in accordance with their form, (*a*) filiform—papillæ filiformes; (*b*) club shaped —papillæ fungiformes; and (*c*) circumvallate—papillæ circumvallatæ. The so-called filiform papillæ are conical, and in the newly born are simple and rounded at their extremity; whilst in adults they are compound, and frequently prolonged into hair-like processes. The clavate or fungiform papillæ are thinner at the basis than at the apex, which appears expanded into a club-like body, and in adults is provided with secondary apices.

The circumvallate papillæ, lastly, are the largest, and are only distinguishable from the fungiform by the wall of mucous membrane which surrounds them; and this is so indistinct in most instances in newly born children, that no differences can be discerned between them and the clavate papillæ. As regards the distribution of these various papillæ on the tongue of man, the papillæ filiformes are spread in nearly equal numbers over the whole dorsal surface of the horizontal part, and on the edges.

The fungiform papillæ are found on the anterior portion of the dorsal surface, and chiefly near the tip and edges; towards the median line of the posterior portion they become more sparing and small, and altogether cease at the root of the tongue. It only happens in some few cases that filiform papillæ are found in the latter region, and still more rarely the fungiform.

The papillæ circumvallatæ are most limited in number; they are placed on each half of the tongue at the junction of the dorsum and the root, and are so arranged that they form a V, the point of which is at the foramen cæcum.

The epithelium both of the upper and lower surfaces is tessellated and laminar; in the filiform papillæ of the tongue of adults the pavement cells are arranged in an imbricated manner, and are provided with longer or shorter processes which project freely beyond the papillæ; the most superficial flattened and horny cells sometimes form solid hairs or fibres, freely projecting beyond the secondary papillæ. The epithelium of the tongue is elsewhere similarly formed to that of other parts of the oral cavity.

The mucosa is thinner in the fore or horizontal part of the tongue in Man, and is, at the same time, much more intimately connected with the subjacent muscles than in the descending portion, where, on account of the abundant loose submucous tissue with numerous glands imbedded in it, it is easily movable; its elements are the same as those of the mucosa in other parts of the oral cavity; fibres of connective tissue being united into fasciculi, and forming a close network that is connected with the deeper tissues by strong trabeculæ.

The so-called septum cartilagineum of the human tongue, which, arising from the hyoid bone, appears as a dense vertical median plate situated between the Genio-glossi, and extending through the whole length ot the organ, gradually diminishing in height towards the apex, is, as Kölliker* has shown, incorrectly named, since it is composed exclusively of connective tissue.

The mucous glands of the human tongue occupy the sides and root of the organ; amongst the former are those described by Blandin† and Nuhn.‡

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* *Beiträge zur Anatomie der Mundhöhle*, *Würzburger Verhandlung*, Band ii., p. 169.

† *Anat. topograph.* Paris, 1834, p. 175.

‡ A. Nuhn, *Ueber eine bisjetzt noch nicht näher beschriebene Drüse im Innern der Zungenspitze*, "On a hitherto undescribed gland in the apex of the Tongue." Mannheim, 1845.

Nuhn found at the apex of the tongue of Man, lying beneath the mucous membrane and a layer of longitudinal muscular fibres formed by the stylo-glossus and longitudinalis inferior, a symmetrically placed pair of glands, from seven to ten lines long, three to four and a half lines broad, and one and a half to two and a half lines thick, opening by five orifices on the lower surface of the apex. N. Ward* once found at this point an azygous gland, placed transversely, one-third of an inch broad, and one-eighth of an inch long, with three fine excretory ducts.

On the lateral border of the tongue, near the styloglossus, there may also be found a median and a more constant posterior group of glands, which either open close to the edge of the tongue, or more rarely in the floor of the mouth.

The glands at the root of the tongue form, beneath the posterior non-papillated portion of the mucous membrane, a continuous layer of six millimetres in thickness, partly imbedded in the musculature.† The excretory ducts of these glands open, in the newly born infant, in the hollows between the ridges; but in adults, in some instances, in the so-called crypts of the root of the tongue, which, according to Salter,‡ constitute reservoirs for the acinous glands. Many of these reservoirs extend, according to this observer, as elongated, sometimes branched, passages for one-half to three-fourths of an inch beneath the surface, and receive at various points the excretory ducts of the mucous glands.

In the wall of these so-called crypts of the root of the tongue, according to Kölliker,§ closed follicles filled with lymph corpuscles are imbedded. He describes each of these saccular glands which receive at their base the excretory duct of an acinous mucous gland, as consisting of a thick-walled capsule, surrounded externally by a fibrous sheath, and lined internally by a prolongation of the oral epithelium. Between these two, and contained in a delicate fibrous, vascular, and at the free surface papillated matrix, lie a number of closed lymph follicles of 0·1 to 0·25 of a millimetre in diameter, forming a continuous, but for the most part single layer.

Huxley ‖ has corroborated generally the correctness of the description given by Kölliker of the glands at the root of the tongue, but finds the crypts of the mucous membrane surrounded, not by closed follicles, but by an indifferent cell containing tissue, traversed by capillaries. Sappey ¶ has only observed the acinous glands opening into the crypts, but not the closed follicles; and whilst Sachs ** is very doubtful of the presence of follicles in the wall of the sacculi, Franz Gauster and Eckhard †† give their support in all respects to the statements of Kölliker.

Gerlach ‡‡ states that he has found follicles in the wall of some only of the lingual sacculi.

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* N. Ward, *loc. cit.*

† Henle, *Splanchnologie*, p. 141.

‡ Todd's *Cyclopædia*, Vol. iv., p. 1140.

§ *Beiträge zur Anatomie der Mundhöhle, Würzburger Verhandlung*, Band ii., p. 177.

‖ Huxley, "On the Ultimate Structure and Relations of the Malpighian of the Spleen and Tonsillar Follicles," *Microscopical Journal*, Vol. ii., p. 74.

¶ *Recherches sur la structure des Amygdales et des glands situées sur la base de la Langue, Comptes rendus*, 1855, No. 22.

** *Observationes de Linguæ structura penitiori*, Vratislav, 1856; and *Zur Anatomie der Zungenbalgdrüsen und Mandeln*, Reichert and Du Bois Reymond's *Archiv f. Anat. u. Physiologie*, 1859, p. 196.

†† G. Eckhard, *Zur Anatomie der Zungenbalgdrüsen und Tonsillen*, Virchow's *Archiv*, Band xvii., p. 171.

‡‡ *Handbuch der Gewebelehre*, 1854, p. 297.

The conclusions at which Arthur Böttcher * arrived, have quite a different tenor. He found

1. That there are some tongues which do not possess any saccular glands.

2. That the occurrence of exceedingly well-developed sacculi is coincident with disease of the mucous membrane.

3. That between these two there are intermediate conditions in which it is often difficult to decide whether a slight elevation of the mucous membrane of the tongue, with a duct in the centre, is to be regarded as a saccular gland or not.

He is therefore of opinion, (1) That in the healthy tongue there are no saccular glands; (2) That these are swellings caused by disease in the immediate vicinity of the ducts of the mucous glands; and that consequently the follicles in their interior are also neoplastic pathological formations.

I am able to corroborate the statement made by Böttcher, that there are some tongues in which no follicular glands are present, and to add that in such cases the mucous membrane in different parts and to a variable extent of the root of the tongue, as well as the loose tissue of the soft palate of the uvula, and of the upper pharyngeal wall, is infiltrated with lymph corpuscles. These infiltrated parts are destitute of a distinct limiting membrane or capsule.

The flat lenticular elevations of the root of the tongue usually present in adults are merely portions of the mucous membrane in which conglobate glandular substance is imbedded. The central orifice they exhibit is the entrance to a little pit which, like the projections themselves, is lined with tessellated epithelium. At the root of the tongue in the newly born infant the mucous membrane presents no saccular glands. It only exhibits here and there in the above-described ridges, between which the mucous glands open, isolated small or larger groups of cellular elements. These are also present at the bases of the papilla of this part, and in the tissue of the mucosa.

The foramen cæcum, situated in the descending portion of the tongue, though not always, and indeed, according to Bochdalek, junior,† only thirteen times in fifty cases, is continued, by its fundus or posterior wall, which presents a larger or smaller opening directed backwards in the muscular substance of the tongue, into a simple or branched cæcal ductus excretorius linguæ, so called because it constitutes the excretory duct common to a large number of mucous glands.

The epithelium of the foramen cæcum is of the ordinary transitional variety; that of its excretory duct, as well as of its cæcal appendix, is cylindrical and ciliated. The foramen cæcum, according to Bochdalek, is *not* formed by an increase in depth of the most posterior papilla circumvallata.

In regard to the lymphatics of the tongue, Sappey ‡ has shown that delicate vessels proceeding from the close lymphatic plexuses of the mucous membrane penetrate into the papillæ, and form a superficial network. According to Teichmann,§ the lymphatics are confined to the mucosa and sub-

* Arthur Böttcher, *Einiges zur Verstandigung in Betreff der Balgdrüsen an der Zungenwurzel*, "A few Observations explanatory of the nature of the follicular glands at the root of the Tongue;" Virchow's *Archiv*, Band xviii., pp. 190—220.

† Bochdalek, junior, *Ueber das Foramen Cæcum der Zunge*, *Oesterreichische Zeitschrift für Heilkunde*, Nos. 36—46.

‡ Sappey, *Comptes rendus*, 1847, p. 26.

§ Teichmann, *Das Saugadersystem vom anatomische Standpuncte.* Leipzig, 1861, p. 113.

mucosa, and form a plexus with coarse deeply situated and more delicate superficial vessels.

In the papillæ filiformes, a few vessels with cæcal terminations, proceeding from a capillary ring, enter some of the papillæ. At the base of the papillæ fungiformes, again, a circular plexus of vessels is found, and lymph capillaries are present both in the circumvallate papillæ and in the adjoining tissue.

The muscular fibres of the tongue are vertical, transverse,* and longitudinal, the first set belonging to the musculus perpendicularis at the apex, to the genio-glossus in the middle, and to the lingualis and hyoglossus at the sides. Between these vertically arranged fasciculi run those of the transversus linguæ, and in part also of the styloglossus, directed in each half of the tongue from the septum towards the lateral surface.

Finally, in immediate proximity with the mucous membrane, are the longitudinal fibres belonging to the longitudinalis superior and inferior, as well as the greater part of the styloglossus. As a general rule, the vertically ascending as well as the transverse fasciculi penetrate into the mucous membrane through those of the longitudinal muscles, becoming, at the same time, considerably thinner. They also decussate with each other, both before they reach the longitudinal fibres, and after they have emerged from them, when they enter into the mucous membrane.

The longitudinal muscles give off several small fasciculi and fibres to the mucous membrane.

In the *cat* the filiform papillæ situated about the middle of the dorsal surface are best developed; they are here also most numerous, and each is prolonged into one or several recurved horny points. Towards the lateral surfaces of the horizontal portion they rapidly diminish in size, and at the edge cease to be distinguishable to the naked eye; so that here the papillæ fungiformes, which elsewhere on the dorsal surface are situated at tolerably regular distances between the filiform, are seen to project as whitish beads, at considerable distances apart. It is only at the most anterior part of the tongue that the filiform papillæ are distributed over its edges, and extend for a short distance on the inferior surface. At the border of that part of the tongue which corresponds to the junction of the horizontal with the descending portion is found a longitudinal series from ten to fifteen in number, of cylindrical filiform, papillæ, capitate at their extremities, of which the centre ones are longer (three millimetres) than either the anterior or posterior (one millimetre). Towards the root of the tongue the filiform papillæ decrease in number and size, and appear in the form of isolated very broad projections, terminating in a short, soft, recurved point.

In *rabbits*, on the dorsal surface of the tongue, as far back as the descending portion, and on the upper part of this, only closely approximated papillæ filiformes are found, which are absent at the edges, except where the horizontal is continuous with the descending portion. Over the well-known whitish elongated oval elevation of the tongue of the rabbit the papillæ are somewhat larger than on other parts of the dorsal surface. Behind this elevation the mucous membrane presents a smooth surface as far as two small projections constantly situated on either side of the median line, and apparently belonging to the papillæ circumvallatæ.

At the junction of the horizontal with the descending portions on the border of each side of the tongue is found a slightly depressed semi-circular spot, the periphery of which touches the posterior part of the oval prominence. The surface is not smooth, but covered with delicate parallel, vertically arranged folds, on a few of which a filiform papilla may be here and there discerned.

This portion, as well as the above-mentioned minute folds at the border of the tongue in man, and the group of papillæ found at the junction of the horizontal and descending portions of the tongue in the cat, correspond to the peculiar organ described by Weber,† and especially by J. C. Mayer,‡ in many mammals under the term of papilla lingualis foliata.

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* Salter, Todd's *Cyclopædia*, p. 1125; and Kölliker, *loc. cit.*, p. 169.

† Weber, in Hildebrandt's *Lehrbuch der Anatomie*, Band iv., 4. Aufl. p. 150.

‡ J. C. Mayer, *Untersuchungen aus dem Gebiete der Anatomie*, etc. Bonn, 1842, p. 25.

The papillæ of the tongue of the rabbit appear considerably shorter than those of man, and this is due to the absence of depressions in the epithelium between them.

The thickness of the epithelium diminishes from before backwards, and also towards the sides; yet, posterior to the oval prominence, is as thick as at the apex of the tongue.

The structure of the mucosa does not differ from that of man. Its thickness also diminishes from the tip towards the oval prominence. At the root of the tongue the fasciculi of muscular fibres situated beneath the mucosa form a rectangular network, in the loculi of which are contained the lobules of the acinous glands. The excretory ducts of these glands penetrate the mucosa in a vertical direction to reach the surface. Numerous small masses of lymph corpuscles are to be met with around and between the lobules of the glands. In the depressed semi-circular portion of the border of the tongue the laminated pavement epithelium is much more attenuated on the margin of the folds than on their sides. The depths of the folds amount to 0·45 of a millimetre, and the mucous membrane projects into them in the form of an acute angle.

The excretory ducts of large acinous glands open into the grooves intermediate to the folds, the relation of which to the muscular fasciculi is similar to that already described in the case of the glands at the root of the tongue. A considerable number of nerves, the fibres of which are all medullated, are contained in the mucous membrane at the bottom of the folds.

The transversus linguæ exhibits a looser arrangement, as it extends from the middle line of the upper surface to the lower, in that its fasciculi describe arches, which diminish in length towards the border of the tongue.

In the tongue of the *frog* the papillæ filiformes are distributed over the whole dorsal surface; towards the posterior cornua they diminish in number and size, and cease at some distance from their apices. There is also a lateral zone of the dorsum extending along the whole length of the tongue, and from two to three millimetres in breadth, which is destitute of papillæ. The fungiform papillæ are similarly arranged. The two forms are most numerous and largest at the anterior part of the dorsal surface. The papillæ filiformes are thin and long, but towards the cornua of the tongue they are somewhat broader. The epithelium, throughout the entire cavity of the mouth, consists of a laminated and ciliated columnar epithelium, with the exception of the apices of the papillæ, where the most superficial cells are short cylinders, destitute of cilia.* Neither Hartmann nor Hoyer† were able to recognize the continuity of the processes of the columnar epithelium covering the papillæ with the connective tissue corpuscles, as described by Billroth ‡ and Axel Key.

On the lower surface of the tongue the epithelium is formed by two or three layers of pavement cells, the most superficial in some parts bearing cilia.

A nerve trunk, composed of dark-edged fibres, occupies the centre of the fungiform papillæ, whilst at their periphery is a capillary plexus opening into a central vessel; situated peripherically also are muscular fibres which frequently undergo division in their passage upwards. Moreover, transversely situated muscular fibres extend into the fungiform,§ and into some of the filiform papillæ, though they can seldom be followed to the apex.

The glands of the tongue of the frog are pretty equably distributed over the whole of the dorsal surface; anteriorly they are more closely assimilated to the type of the acinous glands than posteriorly. The excretory ducts, especially of the anterior part, support laterally and terminate at their extremities in hemispherical enlargements, or they pursue a closely coiled course, and are then more deeply imbedded between the muscles. As a general rule, they are only surrounded by muscular tissue at their fundus.

The glands are lined by columnar epithelium, the cells of which become shorter in the deeper acini. A few of the cylindrical cells near the orifice sometimes support cilia.

At the posterior part of the dorsal surface, and especially on the posterior processes of the tongue, the glands constitute longer or shorter tubes, which are for the most part inflated or irregularly prominent at their fundus. Here also their fundus is im-

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* Leydig, *Histologie*, 1857, p. 307. Axel Key, Reichert and Du Bois' *Archiv*, 1861, p. 228. Hartmann, *idem*, 1863, p. 634.

† Hoyer, *Mikroskopische Untersuchungen über die Zunge des Frosches*, Reichert and Du Bois' *Archiv*, 1859, p. 501.

‡ *Ueber das Epithel der Froschzunge*, Müller's *Archiv*, 1859, p. 159.

§ Waller, *Philosophical Transactions*, 1847.

bedded amongst the muscles which run up from the deeper parts and accompany the gland ducts for a variable distance towards the surface. The cylindrical epithelium with which they are lined behaves in the same manner as that of the glands of the anterior portion.

Division of muscular fibres occurs, to a considerable extent, in the frog as well as in the newt, calf, bat, sheep, goat, and cat, and also in man. In man, Rippmann* saw simple and individual muscular fibres run out into two, three, or even four moderately long branches.

According to Remak,† microscopic ganglia are situated on the branches of the glosso-pharyngeus, and of the ramus lingualis. And he believes the same relations to subsist between the glands and ganglia of the tongue, as between the submaxillary gland and the ganglion submaxillare.

B. Pharynx.

With the pharynx the digestive tract begins to be independent, and at its lower part assumes a tubular character, whilst, at the same time, it is distinctly differentiated into mucous membrane, muscular layers, and an external investing fibrous membrane.

The *epithelium* of the mucous membrane in the portions immediately adjoining the nasal cavity is laminar and tessellated. This form of epithelium extends, according to Schmidt,‡ to the posterior edge of the so-called pharyngeal tonsils, but their anterior portion, as far as the orifice of the Eustachian tube, possesses a columnar and ciliated epithelium. The distribution of the latter in the regions in question is most extensive in the new-born child, extending here over the whole of the upper portion of the pharynx, known as the cavum pharyngo-nasale. In the adult, on the other hand, it never extends over more than the upper third. Both the epithelium and mucosa are similar in their characters to the same structures of the soft palate.

The free surface § of the nasal region of the pharynx, occupying the interspace between the Eustachian tubes, and extending from the posterior portion of the roof of the nasal cavity to the anterior border of the foramen magnum, exhibits in most instances a delicate longitudinal striation, with laminæ or folds separated by deep fissures, which to some extent become united, giving rise to a plexiform pattern; and frequently the surface is covered with low elevations, traversed by a variable number of short, often irregularly running fissures. These folds exhibit numerous whitish poppy-seed-like enlargements, with a considerable number of roundish pores, which are partly recognizable as the entrance to little isolated pits of the mucous membrane, but are chiefly the orifices of acinous glands.

A larger opening, though not constantly present, is found in the lower half of the median line of the roof of the pharyngeal cavity. It constitutes the entrance to the process of the pharyngeal arch which ascends to the body of the occipital bone, and is usually surrounded by acinous glands, but sometimes also by a muscle. It has been named by J. C. Meyer the Bursa pharyngea.

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* Th. Rippmann, *Ueber das Vorkommen von Theilungen der Muskelfasern in der Zunge der Wirbelthiere und des Menschen*, "On the occurrence of Division in the muscular fibres of Vertebrata and of Man;" Henle and Pfeuffer's *Zeitschrift*, 3. Reihe, Band xiv., p. 200.

† *Ueber die Ganglien der Zunge bei Saügethieren und Menschen*, "On the Ganglia of the Tongue in Mammals and in Man;" Müller's *Archiv*, 1852, Heft 1, p. 58.

‡ Schmidt, *loc. cit.*

§ Luschka, *Das adenoide Gewebe der Pars Nasalis des menschlichen Schlundkoppes*, "The adenoid tissue of the nasal portion of the Pharynx of Man;" *Archiv für wissenschaftliche Anatomie*, v. Max Schultze, Band iv., Heft 1, Seite 5—9.

The thickenings or folds of the mucous membrane of the pharyngeal arch, as well as the walls of the bursa above described, consist of a loose vascular tissue infiltrated with lymph corpuscles, exhibiting in parts the same structure as that which we have seen in numerous portions of the soft palate. At those points where the poppy-seed-like bodies are observed, the mucous membrane presents, over a larger or smaller surface, an adenoid structure closely packed with lymph corpuscles. These infiltrated spots, although constructed on the same plan as the lymph follicles, have, like the similar spots at the root of the tongue, where they are more sparing in number and smaller, no distinct investing membrane.

Luschka * has denominated this part, first described by Lacauchie,† the Tonsilla Pharyngea, and he agrees with Kölliker in regarding it as an aggregate of lymphatic glands. Henle,‡ on the other hand, holds it to be conglobate gland substance. It forms a mass of about eight millimetres in thickness, which extends to between the orifices of the Eustachian tubes, from the posterior extremity of the roof of the nasal cavity, with an average length of three centimetres.

The glandular tissue is in great part divided into laminæ with deep intervening fissures, or is arranged in the form of round sacculi, the walls of which, having an average diameter of one millimetre, are lined by ciliated epithelium and a continuation of mucous membrane, communicating with the exterior by a very narrow orifice. The tissue of the mucous membrane covering the arch of the pharynx is differentiated from that of the lower part by the circumstance that it exhibits over surfaces of considerable extent the characters of lymphatic glandular tissue.

The mucous membrane of the middle third of the pharynx, though more sparingly than in the upper portion, is also infiltrated with numerous cellular elements, which are either irregularly distributed through its substance or lie collected into dense masses in a vascular stroma.

In infants the mucous membrane exhibits a great number of oblong nucleated elements, the extremities of which are drawn out into fine pointed processes which penetrate between the fibres of the tissue. This peculiarity may be observed in several parts of the above-described portions of mucous membrane, and appears therefore to be characteristic of an embryonic condition of the tissue. Wherever the epithelium is laminar and tessellated, numerous papillæ, narrow at their base, and clavate at their free extremity, project from the surface of the mucosa, and penetrate the epithelial layers to about half their depth; but where the epithelium of the roof of the pharynx is laminated, and composed of cylinders supporting cilia, the papillæ are altogether absent.

The large *vessels* form a plexus beneath the epithelium, giving off finer branches, which either pursue a longer or a shorter course parallel to the surface, or form loops immediately beneath the epithelium. In the middle third of the membrane in adults, and especially in the lower parts, are numerous papillæ arranged with tolerable regularity. In the upper parts they are in some parts imperfectly developed, and here and there are altogether absent. In the lower third the papillæ are both constantly present and numerous.

In the infant the *papillæ* are only feebly developed, either in the form of

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* Luschka, *Anatomie des Menschen.* Tübingen, 1862, Band i., Abschnitt 1.

† *Traité d'Hydrotomie*, 1853, Tab. ii., fig. 10.

‡ Henle, *Splanchnologie*, p. 146.

slight sinuosities of the mucous membrane projecting into the epithelial layers, or as sharply pointed papillary elevations composed of connective tissue and bloodvessels, especially over those parts of the membrane presenting striæ or folds, which penetrate to a variable extent into the epithelium.

As it approximates the muscular tissue the structure of the mucous membrane becomes looser, forming the *submucous tissue;* and the fasciculi, which constitute a plexus with meshes of various sizes, are arranged in the upper and middle third in a horizontal direction, or run obliquely backwards and outwards between the fasciculi of the muscular layer to the outer fibrous layer, as well as in the opposite direction from this inwards and downwards, some few fasciculi penetrating between the muscles into the submucosa, in which they are gradually lost as they descend. In the lower third, the fasciculi of the mucosa pursue various directions, but those of the submucosa are chiefly directed downwards.

The acinous *glands* of the pharynx, especially in the middle and lower parts of the upper third, form groups, the excretory ducts of which open with wide orifices. The individual glands are oval, with their long diameter parallel to the long axis of the tube. In the lower third they diminish considerably in number, so that at the upper part of this they only occur in an isolated condition, whilst below they are but rarely met with.

The depth of the mucosa varies with the thickness of the glandular layer, but diminishes gradually in the lower third towards the œsophagus. The larger *nerve trunks* lie in the submucous tissue, and run for the most part in a longitudinal direction, whilst their branches form a deep and a superficial plexus, in the latter of which Remak* and Billroth observed the presence of microscopical ganglia.

The *lymphatics* of the pharynx are numerous, and, according to Teichmann,† are directly continuous with those of the nose, oral cavity, trachea, and œsophagus.

The *outer fibrous layer* of the posterior wall of the pharynx, attached above to the base of the skull, extending downwards, and containing a median tendinous fasciculus which arises from the tuberculum pharyngeum, consists chiefly of strong parallel bundles of fibrous tissue, with a variable amount of finer and broader elastic fibres. These for the most part descend obliquely with the fasciculi accompanying the nerves and bloodvessels, and with others derived from the submucous layer form sheaths for the pharyngeal muscles, and give off the secondary septa for the smaller muscular fasciculi.

The *muscular layers* of the posterior, and partly also of the lateral, walls of the pharynx are so arranged as to form an essentially circular external and an internal longitudinal layer. The former is composed of the Constrictores pharyngis, the latter is formed by the Stylo-pharyngeus and Thyreo-pharyngo-palatinus,‡ from the pharyngo-palatine portion of which a few fasciculi are given off which pursue a horizontal direction, uniting on the posterior wall of the pharynx with those of the opposite side to form a series of arches with their convexity directed downwards.

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* Remak, *Ueber peripherische Ganglien an den Nerven des Nahrungsrohres*, Müller's *Archiv*, 1856, p. 189; "On the Peripheric Ganglia of the Nerves of the Alimentary Canal." A contest respecting priority with Meissner, in which it was shown that Remak had previously, in 1840, found ganglia in the tongue and on the pharyngeal branches of the Glosso-pharyngeus.

† *Loc. cit.*

‡ Luschka, Virchow's *Archiv*, Band xlii., p. 485.

A few small fasciculi are also given off from the most internal muscular bundles, especially at the lower part of the pharynx, which, running downwards, penetrate the mucous membrane obliquely, and terminate in it.

The mucous membrane of the pharynx, which is connected by means of short connective tissue fibres with the posterior surface of the larynx, presents the same structure as that of the lower third of the posterior wall.

The glands are here also elongated, and form a continuous layer above, whilst they diminish in number below to such an extent that it is rare to meet with one on the anterior wall of the œsophagus. The excretory ducts of these glands are directed obliquely downwards, so that on examining transverse sections, numerous ducts may be found without any of the glands being present. They become somewhat wider beneath the epithelium, and here possess, lining their interior, a series of well-marked cylindrical cells, subjacent to which are two or three rows of smaller spheroidal cells with comparatively large nuclei.

Adipose tissue is found in considerable quantity in adults, occupying the interspaces of the muscular fasciculi and of the glands of the mucous membrane situated on the posterior surface of the larynx.

c. Œsophagus.

Commencing at the level of the lower border of the cricoid cartilage, the alimentary canal extends, in the form of a completely closed tube, to the foramen œsophageum of the diaphragm. In the undistended condition the mucous membrane forms parallel longitudinal folds, and is attached to the subjacent muscular coat by loose connective tissue.

In Man it is lined by laminated pavement epithelium, the cells of which, both in their form and arrangement, resemble those of the lower part of the pharynx.

The membrana mucosa is situated between the muscular layer of the mucous membrane which commences with the œsophagus, and the epithelium, and it is separated by this muscular layer from the thicker layer of the submucous tissue which occupies the interval between the muscularis mucosæ and the muscularis externa.

In newly born children * the mucosa exhibits in many parts the structure of adenoid tissue. In others, again, numerous bloodvessels are found, running for the most part in a longitudinal direction beneath the epithelium, and accompanied by a sparing amount of connective tissue derived from the external portion of the mucous membrane.

In adults the longitudinal fasciculi of connective tissue derived from the submucosa run inwards between the fasciculi of muscularis mucosæ, and then either pursue a sinuous course parallel to each other, or form plexuses. A great number of cellular structures are constantly found amongst them.

The surface of the mucous membrane is beset in adults with a large number of conical papillæ 0·3—0·5 of a millimetre in length, which project into the epithelium; but in children their presence is only indicated by slight inflections of the line of attachment of the epithelium.

The muscularis mucosæ, or muscular layer of the mucous membrane, consists of fasciculi of smooth muscular tissue running longitudinally, which

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* E. Klein, *Ueber die Vertheilung der Muskeln des Œsophagus*, etc., "On the arrangement of the Muscles of the Œsophagus;" *Sitzungsberichte der k. k. Akad. der Wissenschaften zu Wien.* Mai Heft, 1868.

are only feebly developed in the uppermost part of the œsophagus, where they are separated from one another by large quantities of the mucous tissue; lower down they become coarser and more closely approximated, so that the muscularis mucosæ here forms a continuous muscular layer.

The septa of the several fasciculi are continuous with the mucosa on the one hand and the submucous tissue on the other.

The thickness of this muscular layer is somewhat greater in general in the anterior wall of the œsophagus than in the posterior. The submucous tissue is about four times as thick as the mucosa, and is composed of longi-

Fig. 126.

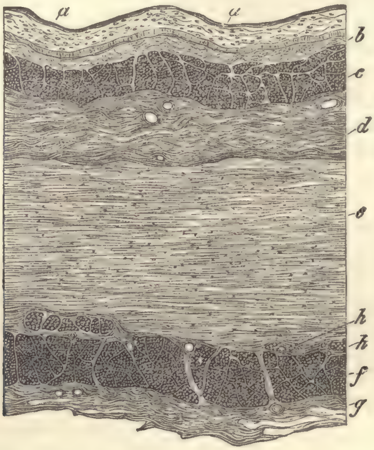

Fig. 126. Transverse section through the lower part of the œsophagus of the newly born Child. *a a*, epithelium; *b b*, mucosa; *c*, muscularis mucosæ; *d*, submucous tissue; *e*, layer of circular muscular fibres; *f*, longitudinal muscular layer; *g*, external fibrous layer; at *h h*, are seen two of the ganglia of Auerbach.

tudinal fasciculi of connective tissue fibres that run parallel to one another, and are always intermingled with finer and coarser elastic fibres. Vessels and nerves derived from the muscularis externa are found in this loose tissue, the nerves running obliquely towards the muscularis mucosæ. The fasciculi of the outer portion of the submucous tissue are directly continuous with the external fibrous membrane, and thus form the septa of the muscularis externa.

Acinous glands are rare and isolated, and less abundant in the posterior wall of the œsophagus than upon the anterior. On the latter they generally decrease in number from above to near the middle, but increase to some extent from this point downwards. They are small and oval, with their longer diameter arranged vertically; they lie in the submucous tissue, close to the muscularis mucosæ, which their excretory ducts penetrate obliquely in a downward direction, opening on the surface of the epithelium with a constricted orifice.

The muscularis externa, or outer muscular coat, is composed in Man of an external longitudinal and an internal circular layer of fibres. The former is arranged in three divisions;* the middle, and by far the strongest, aris-

* Henle, *Splanchnologie*, p. 141.

ing from a triangular elastic membrane attached to the posterior surface of the cricoid cartilage; the two lateral, which partly descend for a short distance internally to the circular layer of the œsophagus, arise from the elastic bundles in which a portion of the Thyreo-pharyngo-palatinus muscle terminates. The longitudinal fibrous layer in its further course is strengthened by the musculus broncho-œsophageus.* The circular fibrous layer gives off on each side the musculus crico-pharyngeus, and receives accessory fibres in the thoracic cavity from the musculus pleuro-œsophageus.† The circular layer continually increases in thickness as it descends, whilst the longitudinal layer, which exceeds the circular layer in thickness in the first fourth, continually diminishes as it descends.

The external muscular layer is not everywhere of equal thickness; in adults it is on the average 1·5 to 2 millimetres thick, and, according to Schmauser,‡ is at the upper part more strongly developed on the anterior wall than upon the posterior,—then diminishes as it descends upon both surfaces, but especially upon the anterior, until in the lower third it is equally developed throughout the whole circumference of the tube.

A few smaller fasciculi, both from the internal circular and from the external longitudinal fibrous membrane are given off, which descend vertically, internal to the former, and external to the latter; the fasciculi are particularly large in the lower fourth, and are derived from the circular layer, becoming vertical as they descend.

The tendons of the fasciculi of the smooth muscular tissue of the œsophagus extend, according to Treitz,§ into the external fibrous membrane. The fibres of the muscularis externa of the upper fourth of the œsophagus in Man are for the most part transversely striated. But besides these, fasciculi of smooth muscular fibres are met with sometimes running vertically external to the longitudinal muscular layer, at others running circularly in the circular fibrous layer, and at others vertically between the fibres of this latter layer.

In the second fourth the smooth muscular fibres are so abundant that they sometimes exceed those of the transversely striated, predominating especially in the anterior wall amongst the longitudinal, and in the posterior wall amongst the circular layers of muscular tissue.

The muscularis externa, in its lower half, is composed of smooth fibres exclusively. Externally the muscular layers are invested by a fibrous sheath composed of connective tissue and elastic fibres, which for the most part run in a longitudinal direction.

At certain parts between the circular and longitudinal muscular fibre layers the nerves form quite a continuous layer, the branches of which perforate the circular muscular coat, in order to reach the submucous tissue. Amongst the nerves running between the circular and longitudinal layers ganglion cells, partly isolated, partly enclosed in a nucleated capsule, are found, as well as groups of ganglion cells united together by means of their processes; moreover, a few ganglion cells occur in the smaller nerve trunks as they run through the mucous membrane. Remak ‖ has described true ganglia as being situated on the œsophageal branches of the vagus.

* Hyrtl, *Zeitschrift der Gesellschaft der Aerzte zu Wien*, 1844, p. 115; and Treitz, *Prager Vierteljahresschrift*, 1853, Band i.

† Hyrtl, *loc. cit.*

‡ Schmauser, *Dissert. inauguratis*, 1866.

§ Treitz, *loc. cit.*

‖ *Ueber peripherische Ganglien an den Nerven des menschlichen Nahrungsrohres*, "On the peripheric Ganglia situated upon the Nerves of the Alimentary Tube in Man;" Müller's *Archiv*, 1858, p. 189.

The lymphatics, according to Teichmann,* partly run in the mucosa, partly in the submucous tissue, but do not form a double capillary network as in the wider portions of the tube.

In the œsophagus of the *Dog* the muscularis mucosæ does not form a continuous layer, as in Man, but first makes its appearance in the middle of the upper fourth, in the form of isolated longitudinal fasciculi, which, in the lower half, surround at various points the acinous glands, and sparingly accompany their excretory ducts nearly to the epithelium. The glands throughout the whole length of the œsophagus form a continuous layer, the thickness of which considerably increases in its lower part.

In the loose submucous tissue, nodal points are scattered, consisting of stellate plexuses of elastic fibres which present a remarkable yellowish-green color.

The outer muscular layer of the œsophagus in the Dog is arranged in a much more complex manner than in Man. It is only in the upper half of the first fourth that it is composed of an external longitudinal and of a stronger internal circular layer. In the lower half of the first and the upper half of the second fourth, both layers are equally well developed, and are composed of fibres decussating obliquely, and at right angles. In the lowest part of the second, and throughout the whole of the third fourth, the inner layer is thinner, and becomes longitudinal, whilst the external is thicker, and is now circular. In the upper half of the inferior fourth, three layers are constantly present: an internal longitudinal; a middle, which is the strongest, circular; and an internal, which is the thinnest, longitudinal. The latter is derived from the internal, but chiefly from the middle, which proceeded above from the external layer. In the lower half of the inferior fourth, three layers are constantly present: an internal oblique; a middle, which is the strongest, transverse; and an external, which is the weakest, longitudinal. The fasciculi of the outer muscular layer do not, therefore, pursue a rectilinear, but a well-marked spiral course.

Smooth muscular fibres first make their appearance at about the commencement of the lowermost fourth of the external muscular layer, but even there they are confined exclusively to the innermost portion, which, immediately above the cardia, is composed of smooth muscular fibres alone. The remaining layers are composed of striated muscular fibres up to the point of entrance of the œsophagus into the stomach.

The nerves are arranged in the same manner as in Man, but they are more numerous. They lie between the internal longitudinal and middle circular layers, and present ganglion cells which are either scattered or are arranged in series one behind the other.

In the *Rabbit* the mucous membrane of the œsophagus resembles that of Man, but its external muscular layer is like that of the Dog. The laminated pavement epithelium increases in thickness downwards. The mucous membrane is generally of looser texture than in Man. When a muscularis mucosæ exists, it is composed of an inner portion, which usually forms a delicate plexus, and a much thicker external portion containing longitudinal bundles of fibres, supporting, especially on its outer surface, large vascular trunks. The papillæ of the mucous membrane are few in number in the upper part, of unequal size, conical, with a broad base; but lower down they become more numerous, so that just below the middle they are in close proximity to each other.

The muscular layer of the mucous membrane is deficient at the commencement of the œsophagus; but at a somewhat lower plane it makes its appearance in the form of small scattered fasciculi, composed of a few unstriated fibres, running in a longitudinal direction, and separated by layers of mucous tissue of considerable thickness. In the lower fourth it forms a continuous layer about 0·04 of a millimetre in width, which is traversed by numerous vessels distributed to the papillæ.

I have not been able to demonstrate acinous glands in the œsophagus of the Rabbit. The external muscular layer, having an average thickness of 0·85 to 0·2 of a millimetre, is composed, like that of the Dog, of spiral fasciculi, which are thus arranged: In the uppermost portion there are two layers, nearly equal in thickness, of which the internal is circular, the external longitudinal in direction. In the second fourth the circular and longitudinal layers run more or less at right angles to their previous course, so that in the third fourth their relative position is entirely changed, and we now find an internal layer, consisting of longitudinal fasciculi, a middle of circular, and an external of longitudinal fasciculi. In the lowermost fourth, although the thickness of these layers differs, their disposition is unaltered. The most internal layer here becomes constantly thinner, whilst the middle and external progressively

* Teichmann, *Das Saugader System*, "The Lymphatic System," *loc. cit.*

increase in thickness. The first two maintain the direction they possess above, but the greater number of the fasciculi of the external layer run obliquely. Unstriated muscular fibres first appear in the lower fourth, and in the external muscular layer of longitudinal fibres; at first, only in the form of small fasciculi, but lower down increasing so remarkably in number and size that they soon outnumber the striated fibres, both in the external longitudinal layer and in the external portion of the middle circular layer. In the lower parts of the inferior fourth the smooth fibres do not merely replace the transversely striated, but occur in great numbers as a new formation, so that these external layers in the vicinity of the cardia exceed the two others in breadth.

Ravitsch * has found the following arrangement of the smooth muscular fibres to obtain in the Horse, Calf, Pig, Cat, and Rabbit.

In the *Horse* the muscular layers of the œsophagus are entirely composed of transversely striated fibres as far as the thickening that is found about 20—25 centimetres above the cardiac orifice; below the thickening, smooth fibres make their appearance in the inner layer, whilst they do not present themselves in the external layer till near the cardia.

In all the above-named animals the transversely striated elements extend in both layers of the œsophagus to a variable distance from the cardia, always ceasing sooner in the inner than in the outer layer. This last statement is, however, opposed to that which, as mentioned above, I have found to occur in the œsophagus of the Rabbit.

Ganglion cells are here still more frequently met with than in the Dog; not only scattered amongst the fibres of the nerves running in the external muscular layer, but also in the lower fourth, in the form of microscopic ganglia, situated between the middle and external muscular layers.

The mucous membrane of the œsophagus of the *Rat* is precisely similar to that of the Rabbit, in regard to all its parts—epithelium, papillæ, and mucosa—as well as in the distribution of the muscular layer of the mucosa. The external muscular layer generally divides into a stronger internal and circular, and a thinner external longitudinal layer. Here and there the external muscular layer exhibits in its lowest portions an internal, strongest, oblique; a middle, circular; and an external, thinnest, longitudinal layer. All the layers are free from smooth muscular fibres as far as the cardia.

The œsophagus of *Birds* presents many points of difference from that of Mammals. In the fowl the mucous membrane is from 0·5 to 0·8 of a millimetre thick, and is covered with laminated pavement epithelium, the uppermost cells of which are tabular, and separated from each other by a broad, remarkably sinuous, intervening substance; those of the middle layers are polyhedral, but rather elongated; whilst those of the deepest layers are spheroidal, but usually somewhat flattened by mutual pressure, and when they surround a papilla, are directed obliquely towards its longitudinal axis.

The mucous layer succeeding to the epithelium is a thick felt-like structure, composed of decussating fibres of varying size. From the surface of the mucous layer numerous small, conical, vascular papillæ project into the epithelium. The glands of the œsophagus are tubular, and are situated in the mucous layer; they are limited externally by the muscular layer of the mucosa, and partially project through that layer with their extremities. The fundus of each exhibits from five to seven or more hemispherical projections, so that they resemble acinous glands. Their excretory ducts, as well as their pullulations, are bounded by a very thin membrana propria, lined by a delicate narrow columnar epithelium. In hardened preparations the cylinders are usually found empty (cup or goblet cells, Becherzellen), the flattened nucleus alone remaining attached to one side.

These glands are always isolated, increase in number towards the crop, and are more sparingly distributed and smaller as they recede from this towards the cervical and the thoracic portions of the œsophagus.

The muscular layer of the mucosa forms a continuous longitudinal layer of smooth fibres, situated external to the mucosa and its glands, and presenting, where it is in contact with the fundus of a gland, a slight projection and attenuation. Here and there small fasciculi are given off, which run for some distance circularly, and then again become longitudinal. The submucous tissue, containing the larger vascular

* J. Ravitsch, *Ueber das Vorkommen quergestreiften Muskelfasern im Œsophagus der Haussäugethiere*, "On the presence of transversely striated muscular fibres in the Œsophagus of domestic Animals;" Virchow's *Archiv*, Band xxvii., p. 413.

trunks in its meshes, is continuous with the mucosa and the external fibrous layer of the œsophagus. The external muscular layer is exclusively composed of unstriated muscular fibres, grouped into larger or smaller fasciculi to form an internal circular, and an external, somewhat thinner, longitudinal layer. Between these two layers is an almost continuous nervous layer, in which are found numerous ganglion cells, either isolated or united into a plexus.

Towards the crop the mucous layer becomes more attenuated, and the glands fewer in number; but the circular muscular layer increases in thickness in relation to the longitudinal. In the crop itself the epithelium presents the same character as in the œsophagus. The mucous layer is here thinner, and there are no glands.

The external muscular layer is more attenuated than in the œsophagus itself. The muscular layer of the mucosa is equal in thickness to that of the œsophagus, and is partially separable into an internal circular, and an external longitudinal layer.

Hasse * found no glands in the cervical portion of the œsophagus nor in the crop of pigeons, but in the thoracic portion flask-shaped glands appeared, with a long narrow neck, and an internal lining of tessellated epithelium. In incubating pigeons he observed a remarkable thickening at the sides of the crop, due to a growth of epithelial cells filled with oil-drops, and resembling those in the milk follicles of Mammals.

In the Newt and Frog the mucous membrane of the oral cavity behind the tongue passes directly into the mucous membrane of the intestinal tract, which has now become converted into a complete closed tube.

The œsophagus of the *Triton* consists of an epithelium, a mucous layer, an external muscular layer, and an investing fibrous membrane. The epithelium, like that of the oral cavity, is columnar. The several cells are conical, with the narrow end more or less prolonged; whilst the base, directed towards the free surface, is beset with long cilia. Their shape may either be simply conical or strongly ventricose near the surface, and then, becoming suddenly attenuated, send a long process into the deeper-lying parts; or they may exhibit, when examined in the fresh state, a nucleated swelling in this process. Between the penetrating processes of the superficial cells fusiform cells are interposed, and between these again are here and there spheroidal cells with relatively large nuclei. In transverse sections of the longitudinal folds of the mucous membrane the penetrating processes of the conical ciliated cells are not directed perpendicularly from the surface, but are curved at their extremities. Hence in many parts these processes appear to be continuous with the elements of the mucous membrane. The mucous membrane consists of broad fasciculi of connective tissue, which present a looser texture toward the external muscular layer, and there form larger meshes, whilst nearer the epithelium the tissue is more compact. Fasciculi of connective tissue penetrate perpendicularly to the surface between the fasciculi of the external muscular layer, decussating once or twice at their entrance into the mucous membrane, and thus forming numerous spaces of considerable size, which are either occupied by thin-walled large vessels, or, being lined with epithelium, probably belong to the lymphatic system. Amongst these fasciculi extending towards the surface are found a variable number of fusiform elements, with rod-like or elongated nuclei. These are directly continuous with the fusiform cells of the innermost fasciculi of the external muscular layer, and are consequently to be regarded as smooth muscular fibre cells.

There is consequently here no independent muscularis mucosæ. In the small and delicate meshes of the mucous layer, large, irregular, or spheroidal masses of protoplasm lie isolated from one another.

The external muscular layer consists exclusively of smooth muscular fibres, the contour of which is either rectilinear or sinuous, and which contain an elongated and often pointed nucleus. It is not everywhere of equal thickness, and does not throughout its whole circumference consist of two distinct layers; on the contrary, the external fasciculi interlace to a considerable extent with the internal, so that in transverse sections a close network of muscular fibres is found, interrupted only by a small quantity of connective tissue. In many instances the direction of the internal fasciculi is horizontal, and that of the external, oblique, or more rarely longitudinal.

There are no glands.

In the œsophagus of the Frog the mucous membrane is lined with ciliated epithelium, similar in thickness and form to that already described in the Triton. In preparations hardened in alcohol, nothing but cup or goblet shaped cells are to be found over tracts of considerable extent.

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* C. Hasse, *Ueber den Œsophagus der Tauben*, etc., "On the Œsophagus of the Pigeon;" Henle and Pfeuffer's *Zeitschrift*, 3. Reihe, Band xxiii., p. 101.

The mucous membrane is strongly developed; its fasciculi pursue a horizontal course parallel to one another from without inwards till they reach the epithelium, beneath which, becoming bent at right angles, they assume a plexiform arrangement. The portion in contact with the external muscular layer, that is to say, the submucous tissue, contains the larger vascular trunks in its meshes.

The acinous glands in the Frog form an almost continuous layer from 0·4 to 0·5 of a millimetre in thickness. The acini vary in size, and are rounded or oval in form. They are lined by an epithelium consisting of closely compressed, rounded, or flattened by mutual pressure, cubical, or cylindrical cells. No muscularis mucosæ exists in the upper part, but in the lower there is to be found in patches situated externally to the glands a not very strong layer of longitudinal smooth muscular fibres, from which, as well as from the circular layer of the external muscular coat of the upper part, a few fasciculi are given off, that penetrate between the glands.

The external muscular coat consists generally of an internal circular and an external longitudinal layer. Fasciculi of fibrous tissue of various size, given off from the fibrous sheath investing the muscular coat externally, penetrate between the muscular fasciculi, forming thin septa, and constituting the support of the larger vessels and nerves as well as of the capillaries and the smallest nervous twigs.

Before we pass to the consideration of the histology of the stomach we must investigate the mode of transition of the several layers of the œsophagus into those of the cardia. In the œsophagus of man the laminated pavement epithelium extends to the cardia, where it ceases with a dentated border, and is replaced by a columnar epithelium. The mucous layer in its more restricted sense becomes rapidly thicker, in consequence of the additional series of glands that here make their appearance; so that the muscular layer of the mucous membrane becomes constantly separated by a greater distance from the epithelium, and at the same time diminishes in thickness.

The submucous tissue in general diminishes in thickness at the cardia, and is divisible into an internal looser and an external more compact layer. In the former lie the great vessels, whilst the fasciculi of the latter penetrate between the fasciculi of the muscularis externa.

There are no acinous glands immediately above the cardia.

The external muscular layer shows the most important changes; the circular muscular fibres which are directly continuous with those of the cardia are most strongly developed just above it; at the cardia itself, and just below it, they again diminish in thickness. The disposition of the longitudinal fibres is similar, except that their fasciculi frequently decussate so that they form a dense plexus. At the same time, after assuming this plexiform arrangement, some of them extend into the circular muscular layer, surrounding its most external fasciculi in order to become still more internal at a lower point. According to Henle,* the longitudinal fibres of the œsophagus partly terminate at the cardia, but the majority are distributed upon the stomach, diverging from one another in various directions. The middle portion of the fibres of the right half of the œsophagus extends uninterruptedly in thick masses along the upper curvature of the stomach; the remainder radiate upon the anterior and posterior walls of the stomach in slightly diverging fasciculi, arranged in a plexiform manner towards the lower curvature, to which, however, they do not reach.

From the left half of the œsophagus only delicate fasciculi extend to the upper border of the fundus. Two sets of fasciculi attach themselves to the right and left diverging longitudinal fibres of the œsophagus, which, slightly curved outwards, and altering their course from the horizontal to the vertical direction, extend over the anterior and posterior surfaces of the stomach. These two single-shaped bands of fibres which decussate in their course

* Henle, *Splanchnologie*, p. 161.

downwards from the cardia upon the anterior and posterior wall of the stomach, are the continuations of the circular fibrous layer of the œsophagus.

The laminated pavement epithelium at the cardia of the Dog is replaced, as in man, by simple columnar epithelium; the mucous layer becomes thinner at the cardia, since the gland tubes there present gradually increase in size. Consequently the muscularis mucosæ, which in the lowermost portions of the œsophagus was situated between the glands for an area of 0.5 millimetre in breadth, becomes more externally placed in order to form a continuous layer at the base of the new series of tubes commencing at the cardia. The acinous glands of the mucous layer of the œsophagus do not cease at the cardia itself, but, becoming at the same time smaller, reach to a distance of three millimetres below the line at which the columnar epithelium of the stomach begins. These are sometimes, although rarely, only the lowermost lobules of a gland, the excretory duct of which opens directly at the boundary line between the œsophagus and stomach, so that above the upper wall at the inner end of the excretory duct the laminated pavement of the œsophagus ceases, whilst below the lower wall the columnar epithelium of the stomach commences. In other cases two rows of acinous glands are found at the commencement of the cardiac portion, the excretory ducts of which open between the tubes with narrow calibre, that here begin to be developed.

The submucous tissue of the œsophagus likewise diminishes in thickness as it passes through the cardia into the stomach. The external muscular layer undergoes the following changes at the same part:—

The fasciculi of smooth muscular tissue of the inner layer of the œsophagus lying next to the cardia, after having remarkably increased in size, and assumed a transverse direction, attach themselves, without any defined line of demarcation, to the circular muscular layer of the stomach, the fasciculi of which are likewise very strong. Those fasciculi of the inner layer that are more remote from the cardia, as they change their direction from the oblique into the longitudinal, enter the external longitudinal coat of the stomach, the innermost portion of which they form. They chiefly consist of smooth muscular fibres, and in order to reach the longitudinal muscular layer of the stomach, run outwards round the transverse fasciculi of the inner layer lying close to the cardia. The middle transverse layer of the lowest portion of the œsophagus ceases almost entirely after rapidly diminishing in thickness at the cardia, only a few transversely striated fibres, with the smaller part of the external longitudinal muscular coat of the œsophagus, passing into the external longitudinal muscular layer of the stomach, the most external portion of which they form. Amongst the transversely striated fibres which preponderate in this external layer are a few fasciculi of smooth muscular fibres. The middle and strongest portion of the external longitudinal muscular coat commences at the cardia itself, and is exclusively composed of unstriated muscle. This layer of smooth muscular fibres is consequently introduced between the fasciculi, chiefly composed of smooth muscles, which are derived from the more remotely situated portions of the internal layer of the œsophagus and the transversely striated muscular fibres proceeding from the external longitudinal muscular tunic.

Immediately after the passage of the œsophagus through the foramen œsophageum, isolated oblique and transversely striated muscular fasciculi are found in the external fibrous sheath. Whether these are derived from the longitudinal muscular layer of the œsophagus, or from the surrounding tissues, I am not at present in a position to determine.

In Rabbits the mucous membrane at the passage of the œsophagus into

the cardia presents the same features as in man; but the external muscular coat differs in some respects both from that of man and that of the dog. For the internal longitudinal fasciculi, after diminishing in number and size, completely cease at the lower extremity of the œsophagus; whilst both the middle circular, and the external longitudinal layers, after they have become entirely composed of smooth muscular fibres, and are increased in thickness, pass each in nearly equal strength respectively into the circular and longitudinal layers of the cardia.

In the TRITON a few acinous glands occur just above the cardia, at the lower extremity of the œsophagus, in the form of a nearly circular zone, and exhibit the same structure as those in the œsophagus of the frog. They pass directly into the tubular peptic glands of the cardia, the excretory ducts becoming shorter, and their acini diminishing in number and size.

The smooth muscular fibres first appearing in the form of small fasciculi around the above-mentioned acinous glands, are arranged where the tubular glands are developed, as an independent muscularis mucosæ, situated externally to the tubes; whilst the fasciculi of the external muscular coat, which in the lower part of the œsophagus are not distinctly separable into two layers, are here grouped into an internal circular and an external longitudinal layer.

The same changes which occur in the œsophagus of the frog at the point of transition into the cardia are here in every respect repeated. The portion of the mucous membrane situated internally to the acinous glands, between them and the epithelium, diminishes in thickness in proportion to the reduced length of the excretory ducts of the glands. At the same time the glands decrease in size, are arranged in closer proximity to one another, and pass by gradual transition into the peptic glands, which are at first vesicular, but subsequently more elongated and tubular at their fundus.

The mucous layer consequently suffers a transposition, in a topographical point of view; for whilst above it is situated between the epithelium and the glands, below it extends between the glands themselves, whilst it diminishes in thickness from the lower end of the œsophagus towards the cardiac orifice.

Immediately above the cardia a muscularis mucosæ is still found external to the glands in the form of partly circular, partly longitudinal or decussating fasciculi of smooth muscular fibres, which, in proportion to the approximation of the glands to the surface, bend inwards in order that, since they always remain attached to the outer border of the glands, they may form a continuous muscularis mucosæ investing the fundus of the gland tubes at the cardia itself.

Where the acinous glands begin to undergo their modification, the submucous tissue of the œsophagus increases considerably in thickness, but again diminishes as soon as the tubular glands make their appearance in the mucous membrane. The external musculature augments in thickness towards the cardia, and is so arranged that, as in the dog, the layer of circular fibres at the upper part of the stomach to a certain extent constitutes a sphincter.

At the cardia numerous fasciculi from the external portion of the circular layer extend obliquely to the inner portion of the longitudinal layer, with which they become continuous after they have decussated with the fasciculi derived from the inner portion of the longitudinal layer, which are directed obliquely downwards into the external portion of the circular layer.

D. STOMACH.

The mucous membrane of the stomach is in general easily movable over the muscular layer, being connected with it by a very loose submucous tissue, and when the stomach is empty, or during the contraction of its muscles, it forms numerous transverse longitudinal folds of various size, meeting one another at oblique angles, and presenting a plexiform appearance. This is particularly well marked in the cardiac extremity and greater portion of the left side of the stomach; whilst in the region adjoining the pylorus, as is very distinctly visible in the rabbit, where the mucous membrane is more intimately connected with the muscular layers, the folds of the former are either altogether absent, or only sparingly present. The epithelium is of the simple columnar variety, and, commencing at the border of the cardiac orifice in man, is equally distributed over the whole surface of the stomach. The individual cells form columnar or truncated cones, and in preparations that have been hardened in chromic acid are, over surfaces of considerable extent, cup or goblet-shaped.

The mucous layer of the stomach in the new-born child increases in thickness, though not quite regularly, from the cardia towards the pylorus; the tubular glands of the stomach are imbedded in it, in close proximity to one another, separated only by a sparing quantity of tissue. At the cardia the glands commence as short indentations of the mucous membrane; but, rapidly increasing in length, soon form cylindrical tubes opening separately, or by a single wider orifice common to two or even three. The fundus of the tubes is in most instances somewhat club-shaped, and more or less curved or contorted, and at the cardiac and pyloric portions it is divided into two or more smaller cylindrical branches. Commencing from the middle of the larger curvature, and proceeding towards the pylorus, the number of tubes in the fundus which do not present division at their extremities usually progressively predominates over those that are divided. At the pylorus itself, the nearer the point of its transition into the duodenum is approximated, the greater is the number of the tubes that assume the elongated simple form.

According to Bischoff,* glands of peculiar form are present in the region of the pylorus; according to Ecker,† the glands are generally only tubular, except those in the neighborhood of the pylorus, which are acinous. Kölliker‡ found in a small zone of the cardia, and in the pale zone of the pylorus, compound tubular, but in the larger middle portion of the stomach, which becomes of a lively red color during digestion, only simple tubular glands.

The columnar epithelium is continued into the gland tubes to a variable depth. The glands at the upper border of the cardia are lined throughout with this form of epithelium. At a distance of from one-half to two millimetres below the upper boundary-line of the cardia, the columnar epithelium lining the tubes is replaced at the fundus of the glands by spheroidal or elongated dark or pale strongly granular cells, often resembling bi-convex lenses. This replacement quickly extends upwards, so that the tubes soon appear to be lined with pepsine cells as far as their uppermost third. This relation obtains approximatively as far as to the middle of the large curvature. Commencing from the middle of the large curvature the columnar epithelium reappears, extending farther down as the pylorus is approached, until at length it replaces the pepsine cells, even at the fundus of the tubes. In this respect there is, however, but little regularity, since tubes may be met

* Müller's *Archiv*, 1838, p. 513.
† *Zeitschrift für rationelle Medicin*, N. F., p. 243.
‡ *Gewebelehre*, pp. 400 and 402.

with not far from the great curvature which are lined throughout with columnar epithelium; whilst, on the other hand, others occur near the pylorus, which, for more than half their extent, are lined by pepsine cells. We constantly meet at the pylorus with many (in some cases nearly all) of the gland tubes, both simple and compound, but especially the latter, that are lined throughout by columnar epithelium, in close proximity to others in which the sides, and in part the fundus, of the tubes are lined with pepsine cells, or next to those in which only the smaller part is covered with columnar epithelium.

Fig. 127.

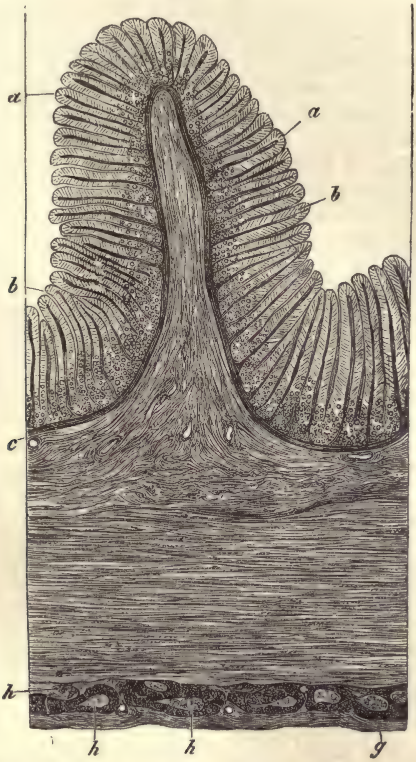

Fig. 127. Transverse section through the fundus of the stomach in a Child. *a a*, cylindrical epithelium; *b b*, peptic tubes; *c c*, muscularis mucosæ; *d d*, submucous tissue; *e*, circular muscular layer; *f*, longitudinal muscular layer; *g*, peritoneum; *h*, ganglion of Auerbach.

In the newly born infant the columnar epithelium generally extends somewhat farther than half-way down the tube. After what has been stated above, it is impossible, therefore, to admit that there is any such distinction of two kinds of gland tubes, one lined by peptic cells, and the other with cylindrical epithelium as has been represented by Henle,* Kölliker,† Donders,‡ and Leydig.§ Gerlach,‖ some time ago, noticed that,

* *Splanchnologie*, p. 157.
† *Würzburger Verhandlungen*, Band iv., p. 52.
‡ *Physiologie*, Band i., p. 204.
§ *Histologie*, p. 293.
‖ *Gewebelehre*, p. 303.

although the columnar epithelium extended to a greater distance down the tubes near the pylorus than at the fundus, still glands may even there be met with, the bottom of which is not covered with this form of epithelial cell. Mayer,* and even Henle † have seen gland tubes in the pyloric region of the stomach of an executed criminal lined throughout with peptic cells. The wall of the glands found in the gastric mucous membrane is structureless. Henle ‡ observed in it, as well as in the membrana propria of other glands, small stellate cells, which, in preparations long macerated in chromate of potash, become smooth and very finely granular. Henle also observed that the cells give off at the plane of the membrana propria from three to ten processes, which run in all directions, and which, whether broad or narrow at their origin, gradually become attenuated and branched, the branches communicating with each other. He therefore considered it probable that these cells are of a nervous nature, although he has in vain endeavored to trace their connection with nerve fibres.

The tissue of the mucous layer is either a fibrous meshwork or adenoid tissue. The fasciculi of fine connective tissue occurring in and traversing the mucous layer in company with the vessels from the submucous tissue which penetrate the fasciculi of the muscularis mucosæ, unite frequently in a plexiform manner between the gland tubes, and include between their fibres a variable number of lymph corpuscles.

An adenoid network of cells, in the meshes of which lymph corpuscles are contained, is also found here and there between the extremities of adjoining gland tubes as well as just below the surface of the mucous membrane.

In newly born infants the muscularis mucosæ, or muscular layer of the mucous membrane, is from 0·01—0·05 of a millimetre thick, and in adults from 0·05—0·1 of a millimetre, and by its continuity separates the mucous from the submucous layer, forming consequently a level layer just external to the extremities of the gland tubes. The fasciculi of this muscular layer of the mucous membrane commencing from the cardia run chiefly in a longitudinal direction, but the internal fasciculi are partly circular and partly oblique, and the external longitudinal or oblique. Where the fasciculi of the one or the other layer run obliquely, they decussate; and if they were in the first instance internal and longitudinal, penetrate, after decussating, into the internal circular layer. They present an inverse relation, if before the decussation they constituted a portion of the internal circular layer; for in that case, after the decussation, they enter into the external longitudinal layers. Both from the internal and external longitudinal layers of the muscularis mucosæ small fasciculi are given off, which extend between the extremities of two tubes into the mucous membrane. Here they either run parallel, or, if they do not pass off at right angles to the muscularis mucosæ, decussate with an adjoining fasciculus, in order then first to break up, forming a kind of pocket composed of smooth muscular fibres running perpendicularly to the surface and embracing the several tubes. The number of muscular fibres constantly diminishes towards the surface. When a few muscular fibres extend as far as the epithelium, they bend in a direction parallel to the surface, and are no longer capable of being followed in the sub-epithelial tissue, or they run between the fibres of fresh fasciculi,

* *Berichte der Freiburger naturwiss. Gesellschaft*, No. 9, p. 147.
† *Loc. cit.*, p. 159.
‡ *Loc. cit.*, p. 46.

which here and there course in a direction parallel to the surface beneath the epithelium.

The submucous tissue which occupies the folds of the mucous membrane resembles that of the œsophagus, and just as the latter stands in relation with the septa of the muscularis externa, and of the external fibrous layer, so it is here in relation with the peritoneal investment, with the septa of the muscularis mucosæ, and with the mucous layer itself.

The thickness of the submucous tissue in the stomach of the newly born child amounts, in hardened preparations, upon the average, to 0·35 of a millimeter.

Lymph follicles, either in the form of glandulæ lenticulares, or aggregated into Peyer's patches, such as have been described as occurring in the stomach by Frerichs,* Bruch,† Bischoff,‡ and Kölliker,§ I have been unable to discover in any of the animals I have examined. It does indeed happen that certain portions of the mucous membrane of adults is more strongly infiltrated with corpuscles than others, but these spots have no definite limiting membrane. They may project to some extent from the surface, and may thus have given rise to the idea of their being proper lenticular glands.

In regard to the *lymphatics* of the stomach, we know from the investigations of Teichmann,‖ that in the dog they form a superficial plexus lying beneath the cæcal extremities of the tubular glands, and a deeper plexus situated between the muscularis mucosæ and the muscularis externa, and consequently in the submucous tissue. In the entire glandular bed no vessels of this kind are present. The vascular plexus above mentioned does not communicate with the capillary lymphatic system of the serous membrane directly, but through the intermediation of trunks provided with valves.

As Remak¶ has shown, and as has been corroborated by many histologists, the *nerves* of the stomach possess numerous ganglia, both in the muscularis externa and in the submucous tissue. I find in newly born children, that the greater number of ganglia are situated between the fasciculi of the longitudinal fibrous layer reaching externally to the peritoneal investment, and internally to the circular muscular layer, and forming, in parts, a continuous chain. In the submucous tissue, as in other parts of the intestinal canal, the nerves form a plexus, in which, as has already been mentioned, numerous ganglia are also found.

The external muscular layer presents, at the commencement of the large curvature of newly born children, a thickness of 0·95 to 1·1 of a millimetre; the circular muscular layer has a thickness of 0·7 to 0·85 of a millimetre. The fasciculi of this last do not here run parallel, but frequently decussate.

The fasciculi of the longitudinal muscular layer give off branching fasciculi, which, after frequent decussation, penetrate in an oblique direction into the circular layer. Smaller fasciculi also penetrate into the submucous tissue; these are continuous with the inner portion of the circular layer, and originate the fibræ obliquæ that will hereafter be described. According to Treitz** they terminate in the mucous membrane, with elastic tendons.

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* Frerichs, *loc. cit.*

† Bruch, *Zeitschrift für rationelle Medicin*, Band viii., p. 276.

‡ Bischoff, *loc. cit.*, Taf. xiv., fig. 4.

§ *Gewebelehre*, p. 403.

‖ Teichmann, *Das Saugader System*, etc., a. a. O.

¶ A. a. O.

** Treitz, *Prager Vierteljahresschrift*, etc., *loc. cit.*

In the greater portion of the cardiac extremity of the stomach, a distinct division of the muscularis externa is to be observed, into an internal circular, and an external longitudinal layer, having a thickness of 0·25 of a millimetre.

In proportion as the pylorus is approximated along the greater curvature, the external muscular layer becomes stronger, which is effected chiefly by an increase in thickness of the circular layer, which amounts in the child to as much as 1·144 of a millimetre. The fasciculi of the latter layer radiate obliquely, both towards the anterior and the posterior surfaces.

The fibræ obliquæ of the stomach, situated for the most part within the proper circular layer, have been accurately examined by Gillenskoeld,* according to whom the layer of oblique fibres is not so sharply defined from the circular as this is from the longitudinal, but the several oblique fibres are continuous with the circular, and each set passes into the other. The oblique fibres form a girdle around the cardia, and run on the anterior and posterior surfaces of the stomach, as far as the antrum pylori. In accordance with his description, two portions of the oblique layer may be distinguished; one superior and horizontal running in a forked manner over the left side of the cardia, and extending to the antrum pyloricum itself, whilst the other consists of shorter fasciculi, that run downwards, and sooner enter the circular layer. At the plyorus itself, when the stomach is continuous with the duodenum, the circular muscular layer in the infant attains a thickness of 2·64 millimetres, whilst the longitudinal layer is reduced to a minimum, the greater number of its fasciculi having entered the circular layer. The passage of the stomach into the duodenum is effected by this sphincter, which constitutes the valvula pylori. With the termination of the sphincter pylori, various changes occur; the gland tubes of the mucous layer become more simple, equal in diameter throughout, and completely lined with cylindrical epithelium. They are now called the Crypts of Lieberkühn.

In the submucous tissue, acinous glands occur in close contact with the muscularis mucosæ (Brunner's Glands), which, at first small, soon increase in size, and penetrate with their excretory ducts the muscularis mucosæ and the mucosa itself. Where the first lobuli of these glands occur, small fasciculi are given off from the external portion of the muscularis mucosæ, which run for a short distance external to the glands, and separate them from the adjoining submucous tissue.

Acinous glands consequently first make their appearance at the commencement of the duodenum.

[In the Dog the tubular glands of the mucosa, like those of man, commence as short involutions of the mucous membrane lined throughout by a continuation of the columnar epithelium of the surface. At the commencement of the cardia they are divided and irregularly dilated at their extremity. About three millimetres lower down they assume the form of simple tubes, slightly dilated at their extremity. At the same time the columnar cells are replaced at the bottom of the tube by secreting cells, which gradually extend towards the opening; the glands coincidently becoming considerably increased in size. The ducts either open separately or several together.

From the middle of the larger curvature the pepsine cells are replaced again by columnar epithelium, in the same manner as in man.

The thickness of the mucous membrane also increases towards the pylorus in the dog as in man. On the inner surface of the longitudinal fasciculi of

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* Gillenskoeld, *Ueber die Fibræ Obliquæ im Magen*, "On the Oblique Fibres of the Stomach;" *Archiv für Anatomie und Physiologie*, 1862, Heft 2.

smooth muscular fibres proceeding from the œsophagus, and on the outer surface of the muscularis mucosæ at the cardia, where the tubular glands begin to be lined with pepsine cells, a layer of circular muscular fibres is superadded, at first feebly developed, but soon becoming thicker. The thickness of the muscularis mucosæ varies; in the fundus it amounts to 0·1—0·25 of a millimetre, and is here distinctly separated into an internal circular and an external longitudinal layer. In respect to their course and decussation, its fasciculi exhibit the same relations as in man.

The quantity of muscular fibres penetrating into the mucous layer between the glands is larger in the dog than in man.

The mucous membrane of the stomach of the Rabbit diminishes in thickness from the cardia towards the fundus, and from this point increases again towards the pylorus. The gland tubes it contains are similar in form to those in the stomach of the dog. In the fundus the individual tubes are a little wider than in the dog, and open by twos or threes into cylindrical fossæ, lined with columnar epithelium, which reach to one-fourth part of the thickness of the mucous membrane. The nearer the pylorus, the farther does the columnar epithelium extend down the tubes; moreover, this, both on the surface and in the tubes themselves, in preparations hardened in chromic acid, is almost entirely composed of cup cells.

The muscularis mucosæ in the cardiac portion consists for the most part of longitudinal fasciculi, becoming somewhat stronger towards and in the fundus, and exhibiting here at most points a circular and longitudinal layer of equal thickness. In the pyloric portion of the stomach the fasciculi of both layers completely decussate with one another, and it is only at certain points that a distinct circular and longitudinal layer can be distinguished. Numerous fasciculi here branch off into the mucosa.

At the pylorus itself the muscularis mucosæ, and especially its longitudinal layer, increases five-fold in thickness. The submucous tissue, which is here, as usual, continuous with the septa of the external and internal muscular coat that dip into the mucosa in company with numerous vessels, is thinner in the pyloric region than at the fundus, and contains in its small meshes numerous spheroidal cells with a relatively large nucleus.

The external musculature consists exclusively, as in man, of smooth muscular fibres, and exhibits the following arrangement: The circular layer is particularly strongly developed at the cardia, but gradually diminishes towards the fundus. The most external fasciculi of the longitudinal muscular layer of the cardia are intimately connected with the fibres of the investing membrane, pursue an oblique direction, and farther down enter the circular muscular layer.

In the pyloric region the relations are altered, and the several layers have not only increased in thickness, but the innermost fasciculi of the circular layer become for a short distance oblique or longitudinal.

At the pylorus itself the muscularis externa presents the same arrangement as in the stomach of the dog.

The nerves and ganglia lying between the two layers of the muscularis externa form in parts a continuous layer, and in parts are sparingly distributed. Ganglia are not very frequently met with in the submucous tissue.

The stomach of the Rat presents remarkable peculiarities of structure. Its left half may be regarded as a continuation of the œsophagus, whilst the right half forms the stomach in the proper sense of the word. The mucous membrane lining the latter portion is of a reddish-brown color on the surface, like that of the fundus of the above-described animals. The two

halves are divided by a fold which commences at the right extremity of the œsophagus that here enters the middle of the small curvature, and is so arranged as to open only into the left half; the communication of its orifice with the right half of the stomach being capable of entire occlusion by this arcuate fold.

The wall of the stomach is considerably thinner in the left half than in the right, at the cost both of the mucosa and of the muscularis externa. It is thinnest in the cæcal dilatation directed upwards, which the left half of the stomach forms at the junction of the large and small curvature. The left half of the stomach may also, from its structural characters, be regarded as a continuation of the œsophagus.

The laminated pavement epithelium increases in thickness from left to right to the summit of the fold, the height of which is about 1·5 millimeter, but again decreases on the right side, the uppermost cells first disappearing by becoming fused into a homogeneous layer; then the middle polyhedric cells vanish, whilst the deepest cells, which are arranged on the fold in the form of palisades and are cylindrical, increase in height, and commencing from the middle of the right side of the fold, cover the mucous membrane as a simple columnar epithelium.

The mucosa, which becomes stronger in passing towards the fold from the right, soon begins to form conical vascular papillæ, which are at first small, but with the increasing thickness of the pavement epithelium towards the summit of the fold increase in height.

The muscularis mucosæ exhibits the most important modifications. It is to it that the existence of the fold is essentially due. The nearer the fold is approximated, the more distinctly does it become differentiated into internal circular and the external longitudinal layers.

The former, rapidly increasing in thickness, ceases after attaining its greatest thickness at the summit of the fold, only the uppermost fasciculi remaining, which are now continued into the circular layer of the muscularis mucosæ of the right half of the stomach. The external fasciculi of the longitudinal layer extend directly as such into the right half of the stomach; the internal fasciculi, however, decussate with the corresponding ones of the right half, and partly penetrate between the fasciculi of the circular layer.

The muscularis externa also increases considerably in thickness towards the fold, attaining its maximum at its base, and then gradually diminishing.

The tubular glands of the right half of the stomach are here also at first short, and lined by columnar epithelium, which, however, is soon replaced by rounded strongly granular pepsine cells, so that the columnar epithelium of the surface only penetrates as far as the upper fourth of the tubes.

The muscularis mucosæ of the right half of the stomach is thinner than that of the left, the fasciculi decussate to a considerable extent, but are here and there divisible into an internal circular and an external longitudinal layer.

The proportion of smooth muscular fibres which are given off into the mucous layer is here also considerable.

Numerous ganglia are situated on the nerves lying between the circular and longitudinal layers of the external muscular tissue.

In Birds the laminated pavement epithelium of the œsophagus ceases at the commencement of the glandular stomach with a dentated border, and is replaced by a simple layer of cylindrical cells.

The flask-shaped and, at their extremities, slightly lobulated glands of the mucous layer of the œsophagus, which have gradually augmented in number from above downwards, cease at the line where the columnar epithe-

lium commences; and the muscularis mucosæ lying external to the mucosa, which diminishes in thickness where the œsophagus is continuous with the glandular stomach, becomes, in consequence of the disappearance of the loose submucous tissue, applied as a longitudinal muscular layer to the muscularis externa, so that it appears to form a single layer with this. In the lowermost portion of the œsophagus more or less sharply defined lymph follicles appear, which are either situated on the outer side of the glands, or externally between these nearly to the epithelium.

The surface of the mucous membrane exhibits a large number of capitate elevations, at the rounded apices of which the orifices of the gland sacs are perceptible. It further presents, in passing from above downwards, a continually increasing number of microscopic villi, minute folds or processes, which nevertheless are only the optical expression of the free terminations of the septa between two adjoining inflections of the mucous membrane, or rather of two adjoining short tubes, opening in immediate proximity with one another.

Bergmann * has described three types of glands: *a.* The well-known saccular glands, presenting a large central cavity, lined with cylindrical epithelium, which receives the orifices of all the smaller tubes lined with gland cells; *b.* A second type, found in the starling, sparrow, yellow-hammer, and crow, in strix flammea and colymbus, in which the several tubes open, by means of secondary ducts, into the principal excretory duct, which last may consequently be very short; lastly, *c.* He constructs a third type of those in which all the several tubes do not open by a common canal into the gastric cavity, but where a number of excretory ducts open in close proximity with one another, and the secretion of which is thus discharged into that cavity. (Cypselus apus.)

Between the extremities of the gland-sacs and the muscular layer a sparing quantity of loose submucous tissue intervenes, which, on the one hand, is continuous externally with the septa of the muscular fasciculi, and on the other supports the vessels, accompanied by which its cords penetrate between the several groups of glands, partly separating their walls, and partly extending into the mucosa. Amongst these fasciculi of connective tissue run, not only vessels which coil around and penetrate between the individual tubes, but also smooth muscular fibres.

In the inferior half of the glandular stomach the simple tubular glands increase in number and size towards the intermediate portion lying between this and the gizzard, in proportion as the gland-sacs diminish in size. The muscularis externa consists of three layers, because at the entrance of the œsophagus into the digestive stomach, the submucous tissue disappears. These are thicker at the point, corresponding to the space between the extremities of two adjoining saccular glands, than in those places where they are directly attached to their convex external portion. At the point of transition of the glandular stomach into the intermediate segment the fasciculi of the outer layers decrease in number and size, but those of the middle and internal layers augment, so that in the intermediate segment the external muscular tunic consists only of an external circular and an internal longitudinal layer.

In the mucous membrane of the *intermediate portion* of the fowl, straight, closely arranged tubular glands are met with, the extremities of which are

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* C. Bergmann, *Einiges über den Drüsenmagen der Vögel*, "A few Remarks on the Glandular Stomach of the Bird;" Reichert and Du Bois Reymond's *Archiv*, 1862, p. 581, fig. *c*.

somewhat narrower than their orifices, and are lined with spheroidal cells which gradually change as they pass upwards into the columnar epithelium of the surface. The tissue of the mucous membrane forms externally to the extremity of the tubes a thin, moderately dense layer, containing a variable quantity of lymph corpuscles, vessels, and nerves.

The muscular tunic consists of an internal longitudinal and an external circular layer; amongst the fasciculi of the latter are a few groups of fat cells.

In the intermediate portion the secretion of the glands becomes hardened into the form of a homogeneous thin layer covering the surface of the epithelium, through which homogeneous bands are prolonged in a vertical direction from the interior of the tubes. This layer investing the surface acquires a peculiar significance in the true muscular stomach or gizzard, where it forms a peculiar horny layer, at first thin, but gradually increasing in thickness as it descends, and when examined in thin sections with transmitted light, presents a deep yellow color. The surface of the mucous membrane invested with this horny and, by reflected light, dark brown layer, forms at the commencement of the gizzard numerous tolerably regularly arranged corrugations, which however diminish in number and height, but increase in breadth downwards. The horny layer everywhere follows these elevations; with the increase of the muscular layer, the horny layer also augments in thickness.

Leydig * originally stated that this layer is secreted by the gastric glands. It consists, in fact, of laminæ superimposed upon one another (consecutively hardened) which are interrupted at the points corresponding to the orifices of the gland tubes, so that these are continued through the horny layer in the form of a canal destitute of walls. It may be distinctly perceived in hardened preparations colored with carmine that a homogeneous band proceeds as a direct continuation of the contents of the tube through the horny layer to the free surface. The columnar epithelium of the mucous membrane immediately subjacent to this layer is continued without interruption into the tubular glands. The several glands exhibit exactly the same structure as those of the intermediate portion.

I am unable, at least in the case of the yellow-hammer and fowl, to agree with the statements of Hasse,† according to whom two kinds of glands are present in the true stomach,—the simple and the compound tubular. The former, like the individual tubes proceeding from the gland-sacs of the crop, are partly lined with tessellated strongly granular cells, and partly with columnar epithelium.

As in the intermediate portion, there follows upon the glandular layer a close web of decussating fasciculi, constituting a muco-membranous tissue. The muscular layer, which at the commencement of this region is still very thin, becoming stronger as it descends by the development of numerous fasciculi, is also limited upon its outer surface, where it is still somewhat thin, by a horny layer in which numerous oblique striæ are perceptible that are continuous with the pointed muscular fasciculi that here take origin. Still more externally succeeds the investing membrane composed of oblique fibres which in some places is composed only of the tendinous expansion of the muscular fasciculi.

Both of the layers situated externally to the muscular layer diminish in pro-

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* Leydig, *Histologie*, p. 309.

† C. Hasse, *Beiträge zur Histologie des Vogelmagens*, "Essays on the Histology of the Stomach of the Bird;" *Zeitschrift für rationelle Medicin*, Band xxviii., p. 1, *et seq.*

portion as that increases, so that where the muscular tissue attains its greatest thickness only a very few small striæ of connective tissue lie on its outer surface.

At the commencement of this region, as in the intermediate portion, the muscular tunic may be divided into two layers, an internal longitudinal, and an external circular layer.

In their further course the former, which constantly receives fresh accessions of oblique fibres from the mucous membrane, becomes first oblique and then circular. The external circular layer is likewise strengthened by numerous fasciculi, originally extending obliquely from without inwards, and arising from the horny layer limiting the muscular tunic externally. A considerable number of vessels and nerves run in the investing sheath of connective tissue.

After the remarks that have been already made respecting the passage of the œsophagus into the stomach of the FROG, little remains to be said in regard to the latter. The columnar epithelium of the surface, which, after treatment with chromic acid, is here likewise almost exclusively composed of well-defined cup cells, the individual cells of which exhibit at their attached extremity a longer or shorter cell process, continues without interruption into the closely approximated tubes of the mucosa. The cells lining the bottom of the tubes are spheroidal and finely granular.

The ciliated epithelium of the œsophagus does not entirely cease at the cardia, but is here and there prolonged for some distance; and even at a much lower level individual ciliated cells may occasionally be met with amongst the non-ciliated. The tubes, which are coiled or lobulated at their extremities, partly open by separate orifices, partly unite by twos in cylindrical pits which, as above mentioned, are lined by cylinder epithelium.

The muscularis mucosæ consists of an internal thinner circular and an external thicker longitudinal layer, the distinction between which is only clearly marked in the lower half of the stomach, whilst in the upper portion the fasciculi of the muscularis mucosæ are almost entirely longitudinal, or decussate to some extent with one another. Everywhere small fasciculi are given off, which penetrate between the tubes into the mucosa.

In the lower portions of the submucous tissue I find isolated, distinctly defined, usually oval lymph follicles, flattened from within outwards, in the capsule of which are contained numerous fusiform cells, with oblong flattened nuclei. Some of the follicles are bounded by the muscularis mucosæ internally, and muscularis externa on their outer side, whilst others, as may occasionally be observed in the intestines of Mammals, penetrate the muscularis mucosæ, and extend to the cylindrical epithelium of the surface.

The submucous tissue itself, like that of the œsophagus, is moderately compact, and about 0·2 of a millimeter thick. The external muscular layer presents, though not uniformly, an internal circular, and an external, much thinner, longitudinal layer.

In some places, instead of the latter, a few oblique fasciculi are found which lower down enter the circular layer. Towards the pylorus both the circular as well as the longitudinal layers which have here become independent, increase in thickness. The nerves and ganglia present the same relations as in the intestinal canal of the Vertebrata.]

E. SMALL INTESTINE.

By E. VERSON.

The small intestine is a direct continuation of the stomach, and, like this, consists of an external peritoneal investment within which are two concentric tubes attached to one another by more or less dense connective tissue. The outer of these two is the muscular coat, the inner is the mucous membrane. The connective tissue forming the bond between them presents various degrees of thickness, but no peculiarities of structure; it contains a few elastic fibres and numerous connective tissue corpuscles.

The relative thickness of the two tubes to one another is too variable to admit of any precise statement being given; but in a general way it may be said that the muscular tunic is about three times as thick as the mucous, and that in Man the thickness of the entire intestinal wall, including the peritoneum, can scarcely be estimated at more than one millimetre. Measurements, however, taken at various parts, will naturally exhibit considerable variations according to the conditions of contraction or relaxation present in the muscular fibres.

The investing peritoneal coat is composed of ordinary connective tissue with elastic fibres, and is either directly applied to the muscular tunic, or is attached to it by means of a small quantity of loose connective tissue. Its free surface is covered by a single layer of pavement epithelium, the cells of which seen in profile appear as thin scales with projecting nuclei.

a. Muscular Coat.

The muscular tunic of the small intestine is differentiated into two superimposed layers, which are distinguished in accordance with the direction of the fibres composing each, into an external longitudinal, and an internal circular. The former pursues the same direction as the intestine itself, the latter runs more or less at right angles to it, and embraces it with circular or spiral coils. A few fibres deviate from these two main directions, coursing round the muscular tube in a radial or oblique direction. Such fibres are occasionally found united into thick fasciculi in the upper portion of the duodenum, close to the pylorus, and they may be followed from thence, forming compressed spirals, into the longitudinal layer of the duodenum.

The muscular tube of the small intestine progressively diminishes in thickness towards the iliocæcal valve, the attenuation being particularly observable in the longitudinal layer, which in some of the lowermost parts may even be altogether deficient. The circular is generally thicker than the longitudinal layer, amounting in the adult to about 0·2 to 0·3 of a millimetre, whilst the longitudinal layer scarcely exceeds 0·1 of a millimetre in thickness. This proportion may, however, be reversed, strata of the longitudinal fibres being here and there found with corresponding diminution of the circular fibres.

The anterior surface of the duodenum is covered, as is well known, by a single layer of peritoneum, whilst the posterior surface is uncovered. At

the lower curvature it is attached to the abdominal wall by an organic muscle, to which Treitz * has applied the name of Suspensorius duodeni. This consists of a few fasciculi of the longitudinal layer, terminating in tendinous fibres, that accompany the dense connective tissue surrounding the cæliac and mesenteric arteries, and are then lost. The fasciculi increase remarkably in breadth, and whilst they do not exceed two to three millimetres in thickness, are almost ten times that breadth. Additional fasciculi not unfrequently join them, derived from the diaphragm (right border of the foramen œsophageum and internal crua).

The duodenum has yet another muscular attachment at the head of the pancreas. In the duodenum of the child I find the pancreas not in all instances sharply defined towards the longitudinal layer of muscles. This last frequently presents areas where acinous groups of the pancreatic follicles penetrate through foramina in it as far as the circular muscular layer, whilst at other points a few muscular fibres are given off from the longitudinal muscular tunic, which penetrate between the acini into the substance of the head of the pancreas. Even the circular layer may thus extend beyond its ordinary limits, and in longitudinal sections made close to the pylorus in the rat I have found a considerable fasciculus of smooth muscular fibres given off from it, which, like the fasciculi already described as entering the head of the pancreas, enter a group of Brunner's glands, and here similarly subdivide amongst the acini.

In its further course the muscular tube presents nothing remarkable, apart from its gradual attenuation, until it reaches the valvula coli. Throughout this, as is particularly observable in the new-born child, only the circular layer passes, whilst the longitudinal layer is interrupted; and indeed the bands of the latter, proceeding on the one hand from the ileum, and on the other from the colon, become considerably attenuated towards the free border of the valve, whilst many muscular fasciculi interlace with each other, and, finally, as my preparations show, arch towards the adjoining circular fibrous layer.

More or less considerable deviations from these arrangements occur in different animals. Thus I may mention, that in the cat the longitudinal fibrous layer does not enter into the formation of the valve, but usually, like the peritoneum, extends uninterruptedly over it. On the other hand, the circular fibrous layer of the small intestine bears the relation to that of the large intestine, of a thinner tube (ileum), which is so introduced through a lateral aperture in the wall of a thicker tube (colon), that it projects with a free border into the lumen of the latter. In the dog, the circular fibrous layer of the small intestine projects in this manner with its free border, but this difference is observable, that the longitudinal fibres appear to be interrupted at the valve.

If a portion of the muscular tube, which can easily be detached with the forceps, be placed in a mixture of one part of acetic acid and ninety-nine of distilled water, or in a solution containing 32·5 per cent. of liquor potassæ (Moleschott), it may easily, after the lapse of a few minutes, be broken up into fibre cells, which, especially after the action of the acetic acid, exhibit a distinct nucleus, with one or two nucleoli. The muscle cells appear smooth, or sometimes angularly folded, and are seldom longer than 0·225 of a millimetre, and broader than 0·005 of a millimetre. No differences can be discerned in the size of the elements forming the longitudinal and circular

* *Ueber einen neuen Muskel am Duodenum des Menschen*, "On a New Muscle of the Duodenum in Man." *Prager Vierteljahresschrift*, Band i.

fibrous layers respectively. In other Mammals, however, they may be both longer and broader, as is remarkably the case also in the Amphibia; those of the Proteus and Salamander being surpassingly large.

The several muscular fibres constituting the muscular tunic of the intestine are held together by a kind of cement. Their larger fasciculi are enclosed by bands of connective tissue, which divide the muscular substance when seen in cross section partly into numerous areas of equal size, and partly into larger segments, which embrace the whole thickness of the muscular tunic.

b. Mucous Membrane.

The mucous membrane constitutes the innermost tube, and exhibits peculiar elevations which project in the form of folds and villous processes into the lumen of the intestine.

Fig. 128.

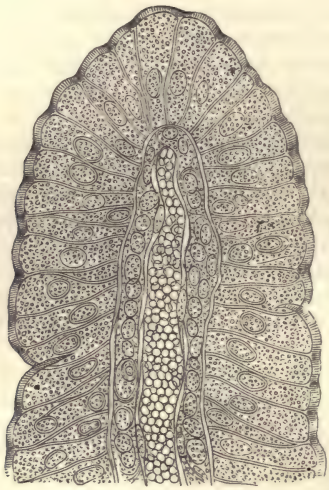

Fig. 128. Section of a villus. From the intestine of a Rabbit. *a*, epithelium; *b*, stroma; *c*, central cavity.

The folds—termed also the valvulæ conniventes of Kerkringius—run more or less at right angles to the long axis of the intestine, and are either parallel to each other, or unite at acute angles, and always become separated by wider intervals towards the lower part of the small intestine.

The folds of Kerkringius are commonly ragarded as persistent formations, because the muscular tunic does not enter into their interior. Nevertheless certain parts of the small intestine occur in children, where the muscular coat presents alternate contractions and relaxations. In the former these folds of the mucous membrane are sharply defined and prominent; whilst opposite the latter the membrane is perfectly smooth, thus affording strong evidence that the folds in question are in some measure dependent upon the contraction of the muscular coat.

The villi of the small intestine, on the other hand, are elevations of the mucous membrane of more limited extent, which make their first appearance in the descending portion of the duodenum, where they are most closely

arranged, and, becoming more and more widely separated from one another, extend to the free border of the iliocæcal valve. They vary considerably in form. Sometimes they are cylindrical; at others conical or clavate, or flattened and expanded like a leaf—variations that in part, at least, are occasioned by the degree of contraction of the general muscular tunic and of their own muscular fibres, to which cause also their variation in length is attributable. In man the length of the villi is from 0·4 to 0·6 of a millimetre, and the breadth from 0·06 to 0·12 of a millimetre.

In every villus one or two, or more rarely three, central spaces are found, constituting the origin of the lacteals. (See Chapter IX. on the Lymphatics.)

The finer structure of the parenchyma of the villi is precisely similar to that of the rest of the mucous membrane, being composed of the tissue termed adenoid tissue by His; that is, of a plexus of anastomosing corpuscles, in the meshes of which cells are contained. These characters are not, however, equally well marked in all classes of animals, and variations may even be observed to occur in one and the same species, in accordance with age, the retiform tissue presenting a more uniform trabecular structure, or forming a delicate plexus of fibres, at the points of decussation of which a nucleus or two only may be discovered, the number of cells contained in the meshes having coincidently undergone considerable diminution. A similar transformation of the adenoid tissue of the mucous membrane may also be observed at certain points immediately beneath the epithelium—a circumstance which has led to the admission of a separate basement membrane, situated between the epithelium and the mucous membrane. No such membrane, however, can either be isolated or shown to form a continuous layer.

Lymph Follicles.—At the free border of the jejunum and ileum roundish or ellipical areas occur, with, in the latter case, their long axes corresponding to that of the intestine, and having a length of 1·5 centimetres, and a breadth of 7·20 millimetres. Their surface is convex, projecting into the lumen of the tube, and has either a few villi scattered over it, or is altogether destitute of them. These are the Peyer's patches, which, when examined with low powers, or sometimes even with the naked eye, appear as a group of roundish, pyriform, or more flask-shaped corpuscles, the so-called follicles. These dip into the submucous tissue with their rounded extremities, whilst their thinner ends form projections on the free surface of the intestinal mucous membrane, and must consequently pierce the muscularis mucosæ, the fasciculi of which, in point of fact, separate to permit the passage of the follicles.

A single Peyer's patch may include twenty or more such follicles lying in close contiguity, and only separated from another by thin prolongations of the submucous tissue. The inferior or deep surfaces of the follicles are somewhat flattened, whilst towards their upper part, especially above the muscularis mucosæ, the lateral boundaries disappear.

When examined with the microscope, these bodies present a remarkable similarity in structure to the so-called medullary cords of the lymphatic glands, and have recently even been regarded, in accordance with the views of Ziegler and Brücke, as really belonging to the system of lymphatic glands. However delicate a section may be that is made through a follicle, only an irregular accumulation of cells can be recognized; but if these be removed by pencilling with a camel-hair brush, or, still better, by agitation of the preparation in a test-tube half filled with water, a network or plexus of

fibres comes into view, similar to, though somewhat closer than that presented generally by the mucous membrane of the small intestine. The follicles consequently are composed of a plexus of fibres and of cells (lymph corpuscles) which fill the interspaces between them. But, just as the plexus of the mucous membrane presents histological differences under various circumstances, so may the framework of intestinal follicles differ, sometimes appearing as a tissue of anastomosing cells, the nuclei of which coincide with the thickened nodal points (child, rabbit), sometimes as a plexus of rigid hyaline trabeculæ (adult man, cat), and sometimes as a fibrous network (young dog).

Fig. 129.

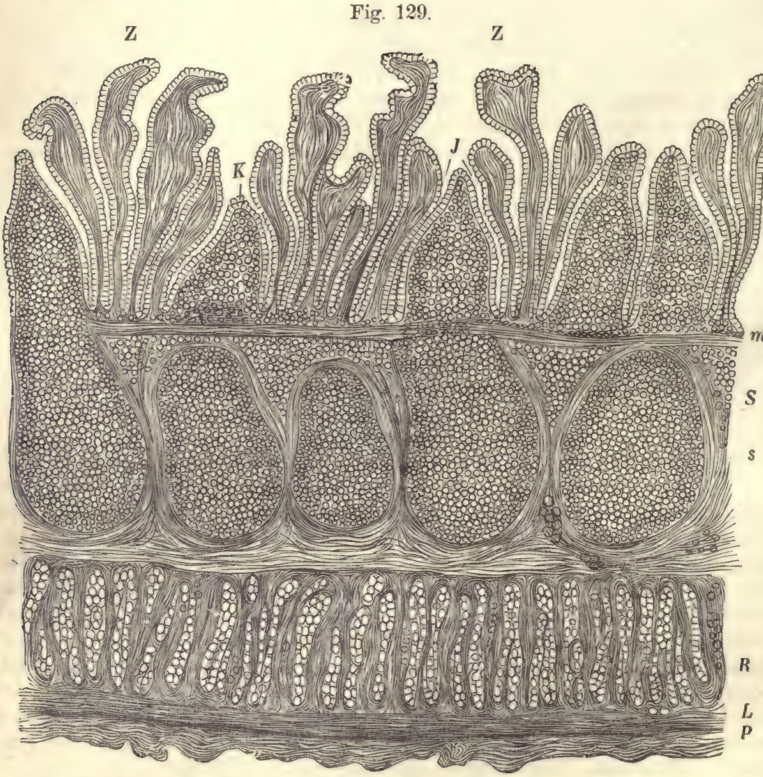

Fig. 129. Longitudinal section of the small intestine of a Rabbit. Z Z, villi; J, cryps; P, a Peyer's patch; K, cap of a follicle; S, submucosa; *m m*, muscularis mucosæ; R, circular muscular layer; L, longitudinal muscular layer; P, peritoneum.

The framework, whatever may be its form, is directly continuous laterally and above the muscularis mucosæ with the reticular tissue of the mucous membrane. In the deeper parts, on the other hand, the meshes gradually become more compact, and either, covered with epithelium, form the boundary of the so-called lymph sinuses, or, where these are deficient, are applied to the dense submucous tissue which constitutes the cord-like septa between the follicles, and extend to near the muscularis mucosæ. But in the event of the septa not reaching so high, the follicles just below the muscularis mucosæ may for a short distance be continuous with each other.

Regarded from another point of view, however, the framework is in direct connection with the vessels of the follicle, and, indeed, not only with the larger ones by means of their tunica adventitia, but also with the most delicate capillaries. This is effected by means of a fibrous network, and in well-prepared specimens the capillaries may be frequently observed to give off processes that suddenly become attenuated into fibres, which coalesce with those of the general mass.

As in man, so in the greater number of animals, the follicles reach the surface of the mucous membrane, and elevate this in the form of a cap (rabbit, sheep, calf, pig). It occurs, occasionally, however, that the follicles do not reach the surface of the mucous membrane, becoming continuous at some distance from it with the ordinary adenoid tissue of the membrane (cat).

Whilst the Peyer's patches constantly occupy the border of the intestine opposite the attachment of the mesentery, isolated or solitary follicles are distributed irregularly over its whole surface. These, like the Peyer's patches, are much more closely arranged in the lowest parts of the ileum. The number of Peyer's patches in the small intestine varies considerably. Authors calculate twenty to be about the average, though no definite limits can be given on either side. Where they are very numerous, they extend into the upper parts of the tube. Middeldorpf observed them even in the lower curvature of the duodenum.

GLANDS.—The secreting glands of the small intestine are constructed upon two different types, the acinous and the tubular, and are named after their discoverers, the former Brunner's glands, the latter, the Lieberkühnian follicles.

Brunner's glands agree exactly in their structure with that of other acinous glands of mucous membranes, and in man form groups of from five to ten acini, which open into a single excretory duct that traverses the mucous membrane, and opens on the surface. The diameter of the acini amounts to about 0·07 to 0·14 of a millimetre, and they consist of a structureless vesicle, the interior of which is lined with somewhat flattened cylindrical cells. The excretory duct is lined by similar epithelium.

The glands of Brunner lie imbedded in the submucous connective tissue, and form small masses, which may however attain sufficient size to cause the whole tunica nervea to disappear; and are bounded on the one side by the muscular tunic, and on the other by the muscularis mucosæ. The latter, however, forms no absolute limit, some of the acini being occasionally found projecting through it against the mucous layer, whilst, on the other hand, a few slender fasciculi of the muscle cells also accompany the connective tissue between the glandular vesicles, and then divide.

The greater portion of the glands of Brunner are found in the vicinity of the pylorus. In man, however, a few groups of these glands are distributed lower down the canal, whilst in other animals the whole series of glands form a single coherent mass. The latter arrangement is remarkably well seen in the rat, in which animal the above-mentioned distribution of the muscular fibres between the gland vesicles can be easily demonstrated.

The *crypts of Lieberkühn* form tubular depressions of the mucous membrane, the blind extremities of which extend to the muscularis mucosæ, and as they are arranged perpendicularly to the surface, they furnish a measure of the thickness of the mucous membrane itself. Their length varies from 0·34 to 0·5 of a millimetre, their diameter amounts to 0·06—0·08 of a millimetre. The crypts are usually held to consist of a structureless membrana

propria lined by a layer of cylindrical epithelial cells. The latter are identical with those forming the epithelium of the intestine generally, and the remarks that have been made respecting these apply to them also. The only slight difference that exist between them is, that the attached extremities of the cells forming the epithelium of the crypts are for the most part broader than the free extremities, which is intelligible when it is remembered that their free surfaces bound a tube of narrower diameter than the cryptic membrane itself.

Fig. 130.

Fig. 130. Crypts and interfollicular connective tissue. From the intestine of the Rabbit. K, crypt; *a a*, epithelium; *d*, adenoid tissue, from which the cells have been removed by pencilling; T, fibrous tissue on the opposite side.

In very fine sections of the intestine, from which the epithelium has been completely detached by delicate brushing, or where the epithelium is accidentally absent, it may easily be demonstrated that the so-called membrana propria of the crypts is not entirely structureless; for from the interfollicular trabecular tissue a few delicate fibrils penetrate into the basement membrane, and, preserving the longitudinal direction of the tube, run towards its orifice, near which they become continuous with a similar but transversely coursing fibrous tissue; this on the other hand, like the branches of a tree, is given off at almost right angles from the septal investing sheaths of the follicles. Such membranes moreover exhibit a beautiful rounded-polygonal pattern, corresponding to the bases of the detached epithelial cells.

The Lieberkühnian follicles occupy the whole free surface of the intestine, with the exception of the basis of the villi and the surface of the solitary glands. But whilst their orifices must necessarily be separated by the former, the tubes dilate beneath them in such a manner as almost again to come into contact, leaving only small interspaces for the passage of vessels and muscular fasciculi. They are usually altogether absent over the follicles, that is to say, of course, where these project into the lumen of the intestine, and here they are arranged like a coronet around the elevations, which has led to the employment of the term corona tubulorum by Johann Müller.

MUSCULARIS MUCOSÆ.—Lying between the mucous membrane and the submucous tissue, Middeldorpf * and Brücke † discovered a layer of organic muscular fibres, which can be traced from one end of the intestinal canal to the other, and from which processes are given off in various directions.

In the muscular layer of the mucous membrane two laminæ of nearly equal thickness may be distinguished, named, in accordance with the prevailing direction of their constituent fibres, the circular and the longitudinal fibre layer, though in some places they run into one another.

The muscular tunic frequently appears interrupted to permit the passage of the lymph follicles, and also to receive the cæcal extremities of the Lieberkühnian follicles; or, lastly, it may itself present a retiform arrangement, and it hence becomes intelligible how sections of the intestine sometimes exhibit continuous layers of circular and longitudinal fibres, sometimes only one of these, and sometimes neither.

We find, also, that in animals the prevalent arrangement approximates to one or other of these types, and I may mention that in the child the circular layer is subordinate, so that the direction of the fibres is almost entirely longitudinal, separating in some places to form beautiful plexuses, whilst in the rabbit the difference in the direction of the two layers is extremely well marked, though they are very thin.

We have already alluded to the processes given off by the muscularis mucosæ in speaking of the small fasciculi situated between the acini of Brunner's glands. Those, however, which pass towards the mucous membrane itself, and were discovered by Brücke ‡ and Kölliker,§ are of greater importance, and are more constantly present. These form, on the one hand, long bands, sometimes not exceeding a single fibre cell in thickness, which run up between the Lieberkühnian glands, and, especially near the free surface of the mucous membrane, are not unfrequently connected by a few transverse fibres; and, on the other hand, strong fasciculi, as many as twelve fibre cells in thickness, which penetrate the villi, and extend throughout their whole length. The muscular fasciculi in some instances enter the villi in the form of separate cords, but in others (especially in the smaller villi) first intercommunicate and diverge from one another at the bases, so that a double layer of muscular fasciculi may almost always be distinguished. One, lying close to the central lacteal, and helping with the epithelium to form its wall, the other running upwards in the parenchyma of the villi,

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* *De Glandulis Brunnerianis, Diss.* Vratisl., 1846.

† *Ueber ein in der Darmschleimhaut aufgefundenes Muskelsystem,* "On a muscular system discovered in the Intestinal mucous membrane;" *Akademie der Wissenschaften in Wien*, Februar-Heft, 1851.

‡ *Loc. cit.*

§ *Ueber das Vorkommen von glatten Muskelfasern in Schleimhäuten,* "On the presence of smooth muscular fibres in mucous membranes;" *Zeitschrift für wissenschaftliche Zoologie*, Heft 1, 1851.

traversing the meshes of the adenoid tissue, and frequently intercommunicating by anastomosing oblique fibre cells (His). The number of such fasciculi may amount to twenty or more in a single villus, as is well seen in the dog and cat, in which the longitudinal section of a villus often presents from seven to ten fasciculi in close proximity.

In the almost mature embryoes of guinea-pigs, instead of completely formed villi, we find solid papilliform masses of cells, with other similar structures presenting a central cavity extending for a variable distance towards the apex. In the latter a band of muscular fibres may be demonstrated, besides a few vascular loops, which, proceeding from the muscularis mucosæ, arch over the apex of the cæcal extremity of the cavity, and return again to the muscularis mucosæ. I have obtained a preparation exhibiting similar features, from an adult cat, and I believe that this affords an explanation of the statement made by Donders,* that transverse muscular fibres are present at the apices of the villi. I have myself not unfrequently seen them in the child, cat, and rat, and refer them to the above-mentioned loop running immediately beneath the free extremity. The fibre cells of the muscularis mucosæ are shorter and more slender than those of the muscular coat of the intestine, being, according to Moleschott, scarcely 0·06 of a millimetre long. The entire thickness of the muscular layer of the mucous membrane in man does not in general exceed 0·021 of a millimetre, but may amount to only one-half of this, or even less.

EPITHELIUM.—The free surface of the mucous membrane is covered with columnar cells, usually arranged in a single layer, but presenting at some points,—as for instance over Peyer's patches,—rounded cells between their attached extremities.

The epithelial cells of the small intestine are sometimes columnar, sometimes conical, and in the latter case are attached by their apices, and present their bases to the cavity of the intestine. They undergo considerable modification from the action of reagents, becoming clavate, irregularly swollen, drawn out into long processes, etc.

The free border of the uninjured epithelial cells of the intestine presents a broad seam or hem, which under favorable circumstances (with good microscopes) exhibits a fine striation running parallel to the long axis of the cell. If the cells have already undergone change, the striæ become irregular, some of the lines projecting beyond the others—others ceasing to preserve their parallel arrangement. It has been a subject of discussion whether these striæ are the expression of fine canaliculi traversing the hem perpendicularly,† or whether they represent small rods of which it is composed.‡ This controversy has to a certain extent lost its importance, as neither the canaliculi nor the rods furnish any satisfactory explanation of the mode in which the absorption of fat molecules is effected.

Besides the ordinary columnar cells of the intestine, and constituting a very remarkable and frequent appearance, are cup, bell, or goblet-shaped structures, the open mouths of which are directed towards the cavity of the intestine, and which contain at their base a mass of protoplasm of variable size with or without a nucleus. Brettauer and Steinach § originally sug-

* *Physiologie*, Band i.

† Funke, *Zeitschrift für wissenschaftliche Zoologie*, Band vi. Kölliker, *Würzburger Verhandlungen*, Band vi.

‡ Brettauer and Steinach, *Sitzungsberichte der Kaiser. Akademie der Wissenschaften*, 1857.

§ *Loc. cit.*

gested that these structures were the results of the metamorphosis of the cylinder cells. It still remains doubtful, however, whether, as Henle* observes, these corpuscles are modified epithelial cells or represent morphological elements of a peculiar kind. The cylinder cells of the small intestine are structures of such delicacy that they can only be examined in the fresh state, without the addition of any reagents, and as they appear on folds of the mucous membrane excised from the living animal, the covering glass being very gently applied. It is only in preparations thus treated that the intestinal epithelium is displayed; it is only possible in this way to obtain a bird's-eye view of the regular mosaic formed by the cells investing the villi from their bases, and it is only thus that we can convince ourselves that both terminal surfaces resemble one another, varying only in their form and size. Even after the lapse of a few minutes, clear bright spots make their appearance at the bases of some of the villi, and in a short time goblet cells become visible. The adjustment of the focus renders it evident that these bright spots correspond to elevations which project at various points to an unequal height above or beyond the general level of the epithelium. Now, in regard to the occurrence of these elevations and the production of spheroidal structures from columnar epithelial cells, already demonstrated by Brücke from examination of cells in profile, there can be no doubt that portions of the contents of these cells are thrown off very quickly after their removal from the living body, and give rise to such cup-like structures. Stricker and Kocslakof have pointed out that a process of this kind is extremely well marked in acute catarrhal inflammation, the columnar epithelium of the catarrhally affected stomach and intestine of the rabbit, even in a fresh condition, presenting throughout tracts of considerable extent cup-shaped cells alone. If we add to this that it not unfrequently happens for the greater part of the intestinal epithelium to become converted, after the action of reagents, into cup cells, we cannot in reason deny that the latter may originate from the ordinary columnar cells.

There is in all this, then, but little that is opposed to the view expressed by Leydig and F. E. Schulze, that the epithelial cells are to be regarded as one-celled glands; for we need only regard the material discharged by the cell as its secretion; and the cell wall, with the remainder of the contained material, as the gland. Further, it may be remarked that up to the present time there is no evidence against the supposition that it is only at a certain period of their development that the cells undergo metamorphosis into goblet cells.

Moreover, at present it cannot be denied that besides the epithelial cells from which the goblet cells already described originate, other peculiar goblet or tubiform structures are present. This has not indeed been absolutely demonstrated, but it constitutes no objection to the view that such structures cannot be seen in the fresh state, and cannot be distinguished from the artificial goblet cells under altered conditions.†

The cup-cell metamorphosis affects not only the cells, but as Basch states, the nuclei; for when the intestinal epithelium of the frog is treated with boracic acid, similar appearances are frequently produced in them. The nuclei are then seen to be ruptured in one or two places, and masses of their contents not unfrequently project from the opening.

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* *Handbuch der Eingeweidelehre*, 1862, p. 165.

† The now extensive literature of this subject is fully given in Eimer's Treatise *Zur Geschichte der Becherzellen*, "On the History of Goblet Cells." Berlin, 1868.

‡ *Centralblatt*, 1869.

Heidenhain * maintained that the attached extremity of the cells of the epithelium of the villi, becoming gradually attenuated, is prolonged into a long process continuous with the connective tissue corpuscles of the parenchyma of the villi. These statements have been accepted, however, by only a few histologists, and have been denied by many.

Amongst the animals best adapted for the observation of the connection of the epithelium of the villi with a subjacent plexus, the guinea-pig may be named. In these animals and in the rat the epithelium of the villi frequently becomes detached from the parenchyma, like the fingers of a glove, and a delicate network then comes into view between the parenchyma and the epithelium, the threads of which are continuous now with the former, now with the latter. The appearances presented, however, are essentially due to manipulation. The network is composed of spheroidal cells, and the transition of such free but closely approximated cells into an apparent plexus may be distinctly followed.

Whether these spheroids are modified red blood corpuscles, or descendants of the epithelial or of some other cells, cannot be satisfactorily determined. Their appearance, and a comparison of them with red corpuscles altered by means of chromic acid, renders the former opinion the more probable one. In these animals then it is certain that no direct communication exists between the epithelium and the stroma.

It is more difficult to speak decisively on this point when the epithelium is not detached, since it is frequently requisite to decide whether two fibres lying in close proximity are continuous with each other.

Nerves.—Two thick layers of ganglionic nervous masses are distinguishable in the small intestine, one of which is situated in the tunica submucosa, and the other between the circular and longitudinal muscular fibre layers. The former, first described by Meissner,† is arranged in the form of a flat layer, although a few ganglia project towards the mucous membrane, and penetrate between the adjoining follicles; the latter, discovered by Auerbach,‡ is more irregular, presenting nodulated ganglionic masses, which are particularly large and numerous where the septa of connective tissue dip into the circular muscular layer.

The several ganglia may attain a diameter of 0·4 of a millimetre, and give off and are traversed by nerves varying from 0·002 to 0·004 of a millimetre in diameter, that form a plexus the branches of which penetrate the circular muscular coat with the septa of connective tissue, and establish a communication between the two ganglionic layers. Other branches pass through the longitudinal muscular layers, to join the mesenteric nerves. A few small scattered ganglia are distributed in the course of these nerves. In regard to the further distribution of the nerves in the mucous membrane, no certain information has been at present obtained, and the same may be said of the mode of termination of the pale nerve fibres in the organic fibre cells of the muscular tunics.

The nerve cells which, accumulated in numbers varying from three to thirty, form the ganglia, are in Man either unipolar or multipolar, and have a diameter of from 0·006 to 0·019 of a millimetre.

The nerves are composed of non-medullated fibres. Both the nerve trunks and the ganglia are invested by nucleated sheaths.

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* *Die Absorptionswege des Fettes*, "The Mode of Absorption of Fat;" Moleschott's *Untersuchungen*, Band iv.

† *Zeitschrift für rationelle Medicin*, Band viii., 1857.

‡ *Ueber einen Plexus Myentericus.* Breslau, 1862.

F. The Large Intestine.

The large intestine is the direct continuation of the small, and exhibits in its several divisions, the cæcum, with the processus vermicularis and the colon, the same structure and arrangement of its constituent parts as are presented by the latter. It is lined by a single layer of columnar epithelium, the individual cells of which not unfrequently vary considerably in size and shape; sometimes they are cylindrical or conical, with truncated apices, and are therefore short and relatively broad, and sometimes they are thin, and externally run into long processes; their nucleus is rounded or elliptical, and either occupies the centre or the lower, *i. e.*, the external, third of the cell. In the newly born child the cylindrical epithelium may frequently be seen to be detached from the subjacent membrane. The thick hem or border of the columnar cells, both in fresh and hardened preparations, presents the well-known fine striation.

The *mucous layer* is similarly formed to that of the small intestine. It is composed of a very close, yet delicate plexus of cells, containing numerous lymph corpuscles in its meshes.

Fig. 131.

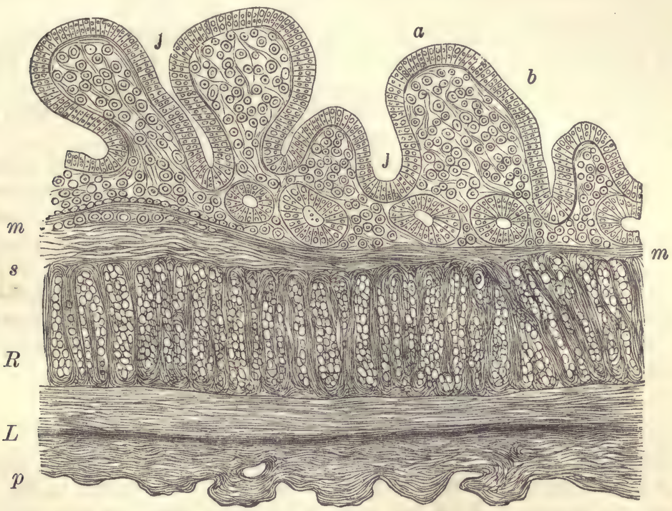

Fig. 131. Section of the large intestine of a Rabbit. J, crypts of Lieberkühn; *a*, epithelium; *b*, mucosa; *m*, muscularis mucosæ; *s*, submucosa; R, circular muscular layer; L, longitudinal muscular layer; *p*, peritoneum.

In the newly born child there are found, besides, numerous fusiform cells, similar to those met with elsewhere in embryonal connective tissue. The Lieberkühnian crypts are imbedded in the mucosa. They form sometimes straight, sometimes slightly curved tubes, arranged either perpendicularly or somewhat obliquely to the surface, generally of equal size throughout, or more frequently swollen at the extremity, and having a diameter of 0·06—0·08 of a millimetre, and a length of 0·35 of a millimetre. The epithelium lining each tube is a direct continuation of the columnar epithelium of the surface, and in no respect differs from it.

As regards the distribution of the crypts, they lie in close apposition in

the cæcum and colon, whilst in the processus vermicularis they are generally separated from one another by wider tracts of mucous membrane, and at the same time appear shorter and broader.

The *muscularis mucosæ* is comparatively feebly developed; its fasciculi are partially arranged into one internal circular and an external longitudinal layer, which generally decussate at the base of the crypts, but frequently give off numerous smaller fasciculi that penetrate the mucosa between the tubes, to which they hold the same relation as in the small intestine.

The *submucous tissue* is looser in texture, and hence forms numerous folds or rugæ in the cæcum and colon, which are capable of being obliterated by extension. The submucous tissue stands here also in connection with the mucosa by means of the septa of the fasciculi of the muscularis externa, and also by the vessels which traverse the muscularis mucosæ.

The *muscularis externa*, like that of the small intestine, is arranged in two layers, an internal circular and an external longitudinal; the conjoint thickness of which in the cæcum and colon of the child amounts to 0·6—0·7 of a millimetre.

The thickness of the longitudinal layer is in inverse proportion to that of the circular; at the longitudinal bands they are both of equal thickness, but in receding from these the circular layer increases as the longitudinal diminishes.

The solitary follicles, as is generally admitted, possess no lacteals; but these, on the contrary, as Teichmann * has shown, are displaced by the follicles, so that their arrangement is much disturbed in their vicinity. The plexus surrounding the follicles consists, as shown by His, of wide lymph sinuses, which are lined by a flat epithelium.†

The *nerves* of the large intestine also present the same general relations as those of the small, both in regard to the plexuses they form between the two muscular layers, and to the ganglionic knots or swellings of Auerbach and of Meissner. The latter are usually spheroidal in form, of relatively large size, but containing singularly small cells.

The cells may be traced in the form of small chains for a short distance in the course of the several nerve trunks. Each nodal point is invested by a layer of connective tissue, in which, besides spheroidal nuclei, fusiform cells with oblong nuclei can be clearly distinguished.

G. Rectum.

The thickness of the intestinal walls constantly augments as the anal orifice is approximated, so that near the middle of the rectum in the adult it attains a thickness of 3—4 millimetres. The proportions are still more remarkable in the newly born child, in which the parietes of the rectum are from 1·3 to 1·5 millimetres thick. This thickening is partly independent and proper to itself, being in fact due to the increase of its own muscular layers, but is in part also attributable to extrinsic causes; the rectum, after leaving the peritoneum, receiving numerous muscular fasciculi from the adjoining parts, and in particular from the musculus levator ani.

The muscular tunics, of which the external here again forms a continuous layer, become in the lowermost parts constantly more and more closely connected with the adjacent tissues; and as the mucous membrane gradually passes into the external skin, the organic muscular tissue of the intestine

* Teichmann, *loc. cit.* His *Zeitschrift für wissenschaftliche Zoologie*, Bände xi., xii., and xiii.; Frey, Virchow's *Archiv*, Band xxxvi.

† v. Recklinghausen, *Die Lymphgefässe*, etc. Berlin, 1862.

blends with the transversely striated muscle in the neighborhood of the anus.

The *peritoneum* also, where it invests the rectum, appears to be thickened, and the submucous tissue, which becomes steadily thicker and denser below, is partly continued directly into the subcutaneous connective tissue of the regio analis, and partly penetrates in the form of bands between the divisions of the musculus sphincter externus.

Fig. 132.

Fig. 132. Longitudinal section of the musculature of the rectum.

Muscular Tube.—The *longitudinal fibrous layer* of the intestine, which again forms a more continuous layer in the rectum, in consequence of the dilatation of the three ligamenta coli, still exhibits in the upper parts considerable differences in its thickness, suggestive of its previous fasciculated arrangement. In the newly born child, at this level, variations occur to such an extent, that in some parts the thickness amounts to 0·23 of a milli-

metre, whilst in others it does not exceed 0·06 of a millimetre; and similar differences occur in the adult. The muscular bands gradually become extended by lateral expansion, decussate in some parts with the outermost fasciculi of the circular muscular layer (at the valves of Houston), and finally become associated with the innermost fasciculi of the musculus levator ani, which, at first separated from them by a thin layer of connective tissue from the posterior portion of the pelvic fascia, ultimately join directly with them at acute angles. A few millimetres higher a few fibres of the posterior portion of the longitudinal muscular layer mutually interpenetrate with those of the musculi recto-coccygei, which, proceeding from the sacrum, here terminate.

Three distinct portions of the musculus levator ani can be distinguished, each of which differs in the nature of its fibres from the other, the innermost being formed of organic, the middle of a mixture of organic and transversely striated, and the external (which constitutes the largest portion) of purely animal fibres. It is only the innermost of these three groups which enters into immediate relation with the rectum, its constituent fibres in part penetrating obliquely into the longitudinal muscular layers, and interweaving with them both in an upward and downward direction, and in part crossing them at right angles, and blending with the circular muscular layer. At the level of the sphincter internus the longitudinal fibrous layer becomes separated to some extent from the former, whilst fasciculi of connective tissue intervene between them; and the limits between the longitudinal muscular layer and the innermost fasciculi of the levator ani, in consequence of their mutual approximation, can no longer be distinguished. The longitudinal muscular layer and the innermost fasciculi of the levator ani radiate out into numerous cords, which penetrate between the fasciculi of the musculus sphincter externus in such a way that the ring of the sphincter externus is split into a series of concentric zones; these traverse its whole thickness, and finally terminate in thin tendons, which are lost in the skin of the buttock.

The *circular muscular layer* at the beginning of the rectum still possesses a considerable thickness. In adults it measures somewhat less than one millimetre, and in the newly born child about 0·2 of a millimetre; but it increases in proportion as the anus is approximated; it forms also temporary thickenings in the lowermost plicæ sigmoideæ, where it interweaves with the longitudinal muscular layer, receives numerous muscular fasciculi from the levator ani, and finally near the anal orifice augments to a thickness of five millimetres in adults, and of 0·5 of a millimetre in the newly born child, causing an annular thickening termed the sphincter internus. The upper margin of this ring is by no means sharply defined, whilst if a longitudinal section be carried through the lowermort part of the rectum, the thickening caused by the sphincter internus is seen to be club-shaped.

Immediately below the sphincter internus, and situated somewhat more externally, the striated fibres of the sphincter externus begin to make their appearance, forming circles round the anal opening, and laterally blending with the most external fasciculi of the levator ani.

MUCOUS MEMBRANE.—The mucous membrane of the lower part of the rectum in man usually presents valve-like processes, running at right angles to the axis of the intestine, but usually extending over only a portion of the circumference. They are neither incapable of obliteration, nor invariably present, though the muscular tissue enters into their formation. In the great majority of cases I found them to be three or four in number,

of which one, and indeed usually the lowest, appeared so far independent that a thickening of the circular muscular layer corresponded to it, amounting to nearly double that which this layer ordinarily presents. In a specimen obtained from a child I found that in this way the circular muscular layer, which at first is 0·21 of a millimetre thick, becomes thickened opposite the fold to 0·4 of a millimetre, the longitudinal layer assisting in its formation by the incurvation of some of its fibres. The lowermost fold is situated about 5—6 centimetres above the anus (1—2 centimetres in the newly born child), and occupies the whole of the right wall of the rectum, and from thence may extend to some distance, both anteriorly and posteriorly. The one immediately above is situated on the left wall, and the next again on the right, and so on at short intervals, alternating from side to side when several valves are present.

The minute anatomy of the mucous membrane of the rectum presents the features as those of other parts of the intestinal tract. Near the anus, however, the elastic fibres become more abundant, the cellular elements more sparingly distributed, the vessels less numerous, and ultimately it passes into the papillated external integument. The muscularis mucosæ may be distinctly followed to the point of transition. This layer also, like all the other tunics of the intestine, increases in thickness in the rectum, so that it may equal, or even exceed, 0·2 of a millimetre, whilst the differentiation of its fibres into an external longitudinal and an internal circular layer is lost in the prevailing longitudinal direction they assume. Near the anal orifice its fasciculi are closely arranged in the form of cords, which cause the projection of the mucous membrane into several longitudinal folds (Columnæ Morgagni), and then become continuous with delicate tendons which terminate in the skin adjoining the anus. The tendinous mode of termination of the muscularis mucosæ is much more easily recognizable in animals than in man, from whom it is difficult to procure sufficiently fresh specimens; in cases where, as in the rat and guinea-pig, the line of transition from the columnar epithelium of the intestine into the tessellated epithelium of the skin occurs abruptly, it exactly coincides with this line.

The ascending processes which are here also given off by the muscularis mucosæ to the interspaces between the Lieberkühnian follicles are connected with each other by a few transverse fibres. These may be constantly seen around the orifices of the follicles immediately below the surface of the mucous membrane.

The *lymph follicles* of the mucous membrane of the Rectum are of the solitary variety, and comparatively few in number. In their general characters they resemble those of the other portions of the large intestine. It is deserving of notice, however, that in the child I met with isolated masses of adenoid tissue below the sigmoid curvature imbedded amongst the interweaving fibres of the circular layer, or lying between these and the longitudinal layer of muscular fibres, which were continuous laterally with the interfibrillar connective tissue of the muscular tunics. It remains to be established, however, whether these perform the same functions as the true lymph follicles.

At the thickened portion of the mucous membrane the *Lieberkühnian crypts* appear to be elongated, their length being as much as 0·6 and 0·7 of a millimetre, whilst they may attain to 0·07 of a millimetre in breadth. In the newly born child they have a height of about 0·3 of a millimetre and a breadth of about 0·05 of a millimetre. The only part of the surface on which they are not found is that over the lymph follicles, on which account the latter appear to be depressed, and can only be recognized with the naked eye

as punctiform hollows. Elsewhere the crypts are situated in close apposition. They cease in the region of the Columnæ Morgagni, in the lowermost part of which a few sebaceous follicles already begin to be visible.

The *epithelium* of the large intestine, in conclusion, presents no points of difference from that lining the small, and like it possesses a striated hem or border. I have, at least, ascertained this to be the case in man, the dog, cat, rabbit, guinea-pig, rat, and frog. Near the anal orifice, however, numerous roundish cells constantly make their appearance between the columnar or conical ones, but this also occurs in many parts of the small intestine. The latter preponderate in number only as far as the Columnæ Morgagni, where they are gradually replaced by several layers of rounded succulent cells the most superficial of which become more and more flattened till the transition into the ordinary tessellated epithelium is completed. In the child this transition is less sudden, because the projecting angles of the folds of Morgagni are already crowned with the pavement epithelium, though the more protected deep fissures between the columnæ always preserve an investment of cylindrical cells. Papillæ are first encountered where the pavement epithelium is completely developed—that is, immediately below the sphincter internus.

In the rat the Columnæ Morgagni are absent, and the lowest crypts extend to the sphincter externus. These lowermost crypts are lined throughout by the usual form of columnar epithelium, but on the side of these orifices which is turned towards the anus a layer of pavement epithelium, four or five cells in thickness, immediately abuts upon the cylinder cells, which last reach to the precise level of the orifice. This point coincides always with that at which the muscularis mucosæ, becoming oblique, runs out into points and is lost.

Nerves.—The plexuses both of Meissner and of Auerbach are continued from the colon into the rectum, the development of the latter preponderating over the former. After the peritoneal investment ceases, the close nervous web from the plexus pudendalis joins it, containing ganglionic enlargements of considerable magnitude. The above plexuses contain both dark-edged and pale sympathetic nerve fibres, which branch and are distributed between the muscular fasciculi of the sphincter internus and externus, and those of the external longitudinal muscular layer and levator ani.

CHAPTER XVII.

BLOODVESSELS OF THE ALIMENTARY CANAL.

By C. TOLDT.

Mucous Membrane of the Oral Cavity.

The mucous membrane of the mouth derives its supply of blood from various branches of the external carotid artery, the arteriæ labiales, buccinatoria, lingualis, transversa faciei pterygo-palatina, and alveolaris superior and inferior. The terminal branches of these arteries enter the submucous tissue of the oral cavity after the trunks from which they proceed have become much diminished in size from giving off numerous branches to the muscles, glands, and other organs, and after having formed numerous anastomoses with each other and the adjoining arterial vessels. After reaching the submucous tissue they are distributed parallel to the surface, and by their numerous anastomoses form a wide-meshed plexus, from which branches extend into the connective tissue layer of the mucous membrane, where they compose a close terminal network, interlacing with the corresponding venous plexus. From this finally the minute branches for the papillæ are given off, the capillaries of which present considerable variety in the different sections of the mucous membrane.

The efferent vessels of the papillæ discharge their blood into a close-meshed venous plexus, which decussates with the above-mentioned arterial plexus. The venous portion of the vascular expansion contained in the connective tissue of the mucous membrane is characterized by the large size of the vessels composing it, their comparatively straight course, and numerous anastomoses, whilst the arterial portion is greatly inferior to the venous in the diameter of its constituent vessels, which are at the same time somewhat less numerous. As a general rule the arterial and venous trunks pursue a parallel course.

The veins arising from the plexus each run by the side of an artery into the submucous tissue, where, having collected together and freely anastomosing with each other, they form a wide-meshed plexus similar to and parallel with that formed by the arteries. These relations are met with throughout the whole extent of the oral cavity, except only that the closeness of the plexus presents considerable variation at different parts, in accordance with the greater or less development of the capillaries of the papillæ.

As a general rule, it may be stated that the larger the papillæ, the more extensive is the capillary plexus in their interior.

At the *margins of the lips*, where the largest papillæ are found, from three to five branches of the terminal arterial plexus enter each papilla, and by their divisions and anastomoses form an elongated but wide-meshed capillary plexus (fig. 133). The transition into the venous channels takes place by one or more capillary loops usually situated at the apex of the papillæ. From this point the small veins, characterized by their large lumen and straight course, receiving lateral branches, and occupying the axes of

papillæ, run towards the centre of their bases, and descend perpendicularly to the venous plexus of the mucous membrane. This course enables them to be easily distinguished from the capillary arterioles which run obliquely towards the papillæ. As we recede from the margin of the lips, the vascular arrangement of the papillæ assumes a more simple character, so that in those of the *posterior surface of the lips* the capillary loops are either simple, or have only one or two transverse branches. The papillæ of *the cheeks*, in like manner, have only simple capillary loops.

Fig. 133.

Fig. 133. Papillæ of the lip.

The papillæ of the *hard palate* are of considerable height anteriorly, yet, for the most part, contain only a single vertical vascular loop; posteriorly, the height of the loops is much diminished, and on the soft palate they form only flat arches, which, originating in the relatively close-meshed plexus of the mucous membrane, present the convexity of their arches to the surface.

The *gums* bear papillæ on their free surface, the vascular plexus of which is nearly as much developed as in those of the lips, but in those of the lateral surfaces there is only a single capillary loop.

The papillæ on the *floor of the mouth* have single loops, with occasionally one or two cross branches.

Langer* has very recently called attention to a remarkable arrangement that is found in the frog. In this animal the capillary vessels of the mucous membrane of the mouth and of the œsophagus as far as the cardiac orifice of the stomach present numerous diverticula, which project towards the free surface of the membrane, and, after becoming constricted, terminate in the capillary vessels. Langer is no doubt justified in regarding these as a peculiar arrangement supplying the place of capillary loops, and adduces, in support of his opinion, the fact that in the toad these diverticula are replaced by the ordinary capillary loops in the posterior parts of the mouth, and in the parts extending beyond to the entrance of the stomach.

* *Sitzungsberichte der k. k. Akademie der Wissenschaften zu Wien*, Band lv., Abtheil. 1; *Ueber das Lymphgefässystem des Frosches*, "On the Lymphatic System of the Frog."

MUCOUS MEMBRANE OF THE TONGUE.

The branches of the lingual artery, of which the dorsalis linguæ is distributed to the upper surface, and the arteria ranina to the middle and anterior portion of the tongue, run obliquely upwards and forwards into its substance, giving off numerous branches in their course, and ultimately, in order to reach the mucous membrane, penetrate the compact layer of connective tissue (fascia linguæ), which invest the muscular mass. On reaching the mucous membrane, these branches break up into a number of terminal twigs, which then pursue a superficial course, and finally form loops in the papillæ.

The simple filiform papillæ of the smallest size contain only a single vascular loop; but all the compound varieties, whether filiform, fungiform, or circumvallate, possess a system of vessels from which a loop is given off to

Fig. 134.

Fig. 134. Filiform papillæ of the tongue.

each secondary papilla. Into every papillæ two or more terminal arterial branches enter (fig. 134), divide in the interior, and then, after anastomosing once or twice, give off a capillary branch into each secondary papilla. The capillary has a diameter of about 0·01 millimetre, and runs to the apex of the papilla, where it forms a loop, and, reversing its course, unites with others to form a venous trunk. The large papillæ contain two or more venous trunks. The larger and smaller papillæ of the same variety, as well as the three subordinate forms of the papillæ, are not in any way distinguishable from one another by the arrangement of the bloodvessels, but essentially by the greater or less development of the vascular plexus, and the number of loops that are given off in each instance in correspondence with the number of the secondary papillæ.

The veins of the papillæ, which are of considerable size in the circumvallate variety, run vertically downwards, and form by their junction with those from other papillæ, and by their frequent anastomoses, a beautiful venous plexus situated between the terminal expansion of the arteries and the fascia linguæ. The meshes of this plexus are usually rounded in the anterior part of the tongue; the larger trunks arising from it penetrate the fascia, and, running side by side with the arteries, receive numerous veins

from the muscles, and dip into the substance of the organ, where they coalesce to form the large venous trunks. In the posterior part of the tongue, numerous large veins take origin from the above-mentioned venous plexus, and, after running for some distance backwards on the fascia, combine at the root of the tongue to form the venæ dorsalis linguæ. The posterior parts of the mucous membrane of the tongue are consequently extraordinarily rich in veins.

It only remains to be mentioned that both the arterial and venous system of the mucous membrane of the right and left halves of the tongue are everywhere in direct communication at the median line.

Saccular Glands of the Mouth and Pharynx, and the Tonsils.

Arterial branches penetrate at various points through the fibrous sheath of the saccular glands into their interior, and give off branches which supply the adenoid substance. Where this last is distinctly divided into follicles, the capillaries are distributed as in those of the intestine (to the description of which the reader is referred), except that their diameter is somewhat greater. But where the adenoid substance is diffused, the vascular plexus is quite irregular. The veins issuing from it are very numerous, and form short broad vessels, which for the most part run in the intermediate spaces of the adenoid substance, as well as immediately beneath the fibrous investment, from which they finally emerge at various points.

Arterial branches also pass towards the mucous membrane, covering the sacculi internally, running up the interspaces between the follicles, or traversing the layers of adenoid substance, and finally terminating in flat capillary loops, which supply the papillæ. From these large venous trunks arise, which unite with those originally in the adenoid substance.

The bloodvessels in the several follicles of the tonsils exhibit the same relations; the larger arterial and venous trunks running and branching between them.

Acinous Glands of the Alimentary Canal.

All the various glands of the digestive tract present an essentially similar arrangement of their bloodvessels; as may be seen in the mucous glands of the mouth, pharynx, and œsophagus, the salivary glands and pancreas, and the glands of Brunner in the duodenum. The larger bloodvessels distributed to these glands ramify in the connective tissue investing the lobules. A single arteriole and veinlet penetrate each of the smallest follicles, then break up in a tree-like manner, and are finally lost in the capillary plexus. The capillary plexus everywhere consists of arched, frequently branched tubules; with a mean diameter of 0·008 of a millimetre, which are so arranged around the glandular vesicles that each of the latter is surrounded by from two to four such arches. These vessels communicate uninterruptedly throughout the entire lobule; each lobule thus possesses its own circumscribed capillary system. A round-meshed capillary plexus invests the excretory ducts of the mucous follicles as far as their orifice; the ducts are also accompanied by two veins which here and there communicate, and near the surface of the mucous membrane usually join by means of an anastomotic ring with the venous plexuses of the mucous membrane.

Mucous Membrane of the Pharynx.

The upper parts of the pharynx receive their supply of blood through

the pharyngo-palatine and spheno-palatine branches of the internal maxillary artery, whilst the middle and lower parts are supplied directly from the external carotid by the ascending pharyngeal and palatine arteries. The terminal branches of these vessels run obliquely towards the surface of the submucous layer, where they ramify, ultimately dividing into fine branches that run immediately beneath the epithelial layer of the mucous membrane. Capillaries, having a diameter of 0·006 of a millimetre, are given off from these vessels, which form simple loops in the serially arranged papillæ. There is scarcely any region where papillæ are found in which the vascular loops present so much uniformity as here. The descending portions of the loops unite into veins that quickly acquire a considerable size, and these vessels communicate by numerous anastomoses, and run for the most part in the direction of the long axis of the pharynx, so as to form a plexus with elongated meshes. Sooner or later the larger venous trunks join the veins of the subjacent glandular or muscular layer. The excretory ducts of the mucous glands are surrounded at their orifices with circularly arranged papillary loops.

Fig. 135.

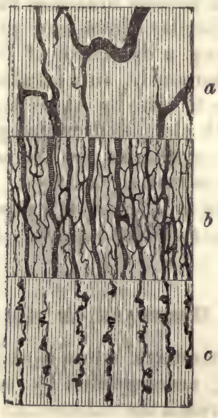

Fig. 135. Submucous and mucous layers of the œsophagus, as seen with different focussing.

Mucous Membrane of the Œsophagus.

The vascular plexus of the mucous membrane of the œsophagus, derived from the œsophageal arteries, and from small branches of the inferior thyroid and bronchial arteries, is extremely close. The large vessels run longitudinally in the submucous layer, communicating from time to time by transverse anastomoses (fig. 135. *a*). The smaller branches reach the mucous membrane obliquely, and then usually become longitudinal and very sinuous in their course; they also form a plexus with elongated meshes (fig. 135, *b*), from which the capillary loops, destined for the most superficial layer, arise (fig. 135, *c*). In the upper part of the œsophagus these last are very similar to those of the pharynx, but are less uniform near the middle. Here the capillaries form flatter arches, with their convexities towards the surface, from which two to five short loop-like processes arise. In the lower parts of the œsophagus the simple loops are again found; they become more vertical, their height gradually increasing

towards the stomach, so that near the cardiac orifice they attain a considerable size. At the point where the mucous membrane of the stomach commences they suddenly cease with a dentated border. The venous trunks of the superficial regions of the mucous membrane accompany the corresponding arteries throughout their whole course.

Muscular Coat of the Alimentary Canal.

The layers of smooth muscular tissue investing the alimentary canal from the œsophagus to the rectum, possess a vascular system proper and peculiar to themselves. The larger vessels reach them by two routes: on the one hand, branches are given off from the vessels supplying the intestine, which penetrate the muscular tunic, and run for some distance between the longitudinal and transverse layers, to both of which their branches are distributed. On the other hand numerous vessels from the submucous plexus turn outward to the internal muscular layer, and penetrate the interspaces of its constituent elements. In the musculature of the stomach, which does not present quite such a regular arrangement, the larger bloodvessels nevertheless likewise run between the several layers and fasciculi.

The ultimate arterial and venous branches run transversely to the direction of the longitudinal muscular fibres, and give off numerous long capillaries at right angles, having a diametèr of 0·007 of a millimetre; these, frequently branching dichotomously, run parallel to the muscular fasciculi, and communicate from time to time by short transverse branches. A very regular capillary system with elongated rectangular meshes is thus formed. If the muscles contract, the capillaries are thrown into curves, so that their characteristic appearance is essentially altered.

The vascular plexus of the muscularis mucosæ exhibits a similar arrangement; but, on account of the smaller thickness of the muscular layer, appears to have very large meshes.

Mucous Membrane of the Stomach.

The bloodvessels of the stomach enter it at the attachment of the peritoneal layers; each artery, accompanied by its corresponding vein, perforating the muscular tunic to reach the submucous tissue, in which they run for a variable distance, constantly giving off branches, or dividing dichotomously; the terminal branches of adjoining arterial trunks form frequent anastomoses. The smallest arteries traverse the muscularis mucosæ to reach the glandular layer, and divide into arcades of fine vessels, having an average diameter of 0·005 of a millimetre, which, winding spirally round the several gland tubes (fig. 136), give origin to new arches, that do not, however, diminish in size. Every gland tube is thus surrounded by a system of capillary arches, which extends nearly to the surface of the membrane. At the same time it must not be supposed that each follicle possesses its own independent capillary system; for, in point of fact, the capillary arches surrounding one freely communicate with those of the adjoining follicles. The rootlets of the veins commence near the orifices of the glands, in the form of thick arches, which run sinuously towards the surface, and there unite to form smaller trunks. Several such trunks converge under the surface of the membrane to form a larger vein, which then descends vertically through the glandular layer. These vertical veins enter at right angles into a wide polygonal-meshed venous plexus, which lies above the terminal expansion of the arteries, situated between the muscularis mucosæ and

the glandular layer through the whole extent of the mucous membrane of the stomach. Inasmuch as this plexus is exclusively composed of tubes of larger calibre, and is also exclusively fed by the above-described veins, it can be distinguished with remarkable facility when seen from the surface, as in fig. 137, from the arborescent terminal expansion of the arteries. From this venous plexus larger vessels take origin, which perforate the muscularis mucosæ, join the arteries, and accompanied by them, traverse the submucous tissue, where they unite with others to form strong vessels that perforate the muscular tunic of the stomach.

Fig. 136.

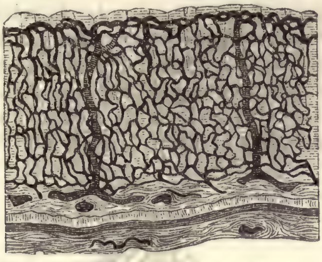

Fig. 136. Vessels of the walls of the stomach, as seen on transverse section.

Mucous Membrane of the Intestine.

With the exception of the large intestine, the arrangement of the bloodvessels of the mucous membrane throughout the whole extent of the alimentary canal is essentially similar, being modified only by the number and size of the villi, the distribution of the glandular follicles, Peyer's patches, etc. The arteries reaching the intestine between the layers of the mesentery perforate its muscular coat with the accompanying veins, and run in the submucous tissue chiefly at right angles to the axis of the tube. They communicate with each other by longitudinal and oblique branches, and form a wide-meshed plexus. The venous trunks accompanying them likewise form

Fig. 137.

Fig. 137. Vascular plexus of the stomach, seen from the surface.

a plexus, which may be distinguished from that of the arteries by the more frequent anastomoses and the larger size of the vessels. If the intestine of

the mature fœtus of the rabbit after injection be divided along the attachment of the mesentery, and the flat surface examined, this vascular network appears in the form of extremely delicate arcades, which, commencing at the attachment of the mesentery, extend on either side about one-third around the whole circumference of the intestine. Beyond this point the arteries and veins pursue a separate course.

The numerous branches proceeding from the submucous *arterial* expansion divide, after they have traversed the muscularis mucosæ, and have reached the glandular layer of the Lieberkühnian follicles, into capillary arches, which coil spirally around the glandular tubes, are about 0·007 of a millimetre broad, and extend to the surface of the mucous membrane, whence branches pass off to the villi. Other arterial twigs ascend without branching between the gland tubes to supply the villi.

There are no proper *veins* formed from the capillaries surrounding the tubular glands, but the vessels collectively transmit blood into the capillaries of the villi. We must therefore regard the capillaries of the intestinal mucous membrane and of the villi as forming a common system, except that the latter receive special accessory arterial branches. The capillary system of

Fig. 138.

Fig. 138. Vascular plexus of the intestinal mucous membrane, seen in transverse section.

the villi lies close to the surface, being separated from the epithelium by only a delicate homogeneous layer, and is tolerably close (fig. 138). It consists essentially of tubes, averaging 0·009 of a millimetre in diameter, which pursue a slightly tortuous course in the long axis of the villi, and communicate by numerous transverse tubules.

The arterial twigs above alluded to, arising directly from the vascular plexus of the mucous membrane, run singly or several in number to the villi, in which, after a short course, they break up into capillaries, and their terminal branches, after forming loops, may frequently be seen to enter the venous radicles. The relative numerical proportion of the longitudinal and transverse capillary branches of the villi varies considerably in the intestines of different subjects, sometimes one and sometimes the other preponderating. The arrangement of the capillary plexus is also modified by the form of the

villi. In those that have a flat conical shape, as in the duodenum, the transverse branches are usually smaller in number, whilst in cylindrical villi the longitudinally running vessels are less developed, and the transverse branches are consequently more numerous. In strongly contracted villi the capillary plexus appears closer, and the vessels more tortuous. The plexus is usually also more close near the apices of the villi. By the union of several arches of capillary vessels the venous radicles here originate, and, speedily coalescing, form a venous trunk of considerable size, which descends vertically through the villus, and joins with the veins of neighbouring villi.

In their further course the veins thus formed descend through the glandular layer without receiving any other branches or forming anastomoses, and finally terminate by entering the venous plexus lying subjacent to that layer. Where the villi are absent, as in the large intestine, the transition of the capillary plexus into the veins occurs in a precisely similar manner at the free margin of the folds which the mucous membrane forms around the opening of the tubular glands. The arrangement of the venous expansion beneath the Lieberkühnian glandular layer differs essentially from the arterial. Whilst the arteries break up in an arborescent manner into fine meandering branches, the veins are formed from the large venous trunks that descend from the villi. The venous plexus of the intestine is distinguished from the analogous one of the stomach by the more sharply defined limitation of the territory belonging to the several venous trunks, and by the more sparing occurrence of anastomoses.

In the large intestine the arrangement of the bloodvessels is similar to that of the stomach, with the exception that the capillary system surrounding the glandular layer is not so much ramified, so that in many parts only straight and but little branched tubules are found between the glands from which the close superficial venous plexus proceeds. The trunks collecting the blood from these extend downwards through the glandular layer, and discharge themselves, like those of the stomach, into a wide-meshed plexus of large veins in the deepest layers of the mucous membrane.

Solitary Gland Follicles and Peyer's Patches.

These obtain their vascular supply from the submucous plexus of the intestine. The arterioles destined for *the follicles* proceed in part directly from the branches of the submucous plexus, and are partly branches of those trunks which break up into capillaries for the layer of tubular glands. The former chiefly run towards the base, the latter to the lateral surfaces of the follicles. The capillary system (fig. 139) consists of a plexus of vessels having a diameter of about 0·008 of a millimetre, with rounded polygonal meshes, which invests the whole surface of the follicle. From this plexus numerous fine capillary branches of 0·004—0·006 of a millimetre in diameter pass radially into the interior of the follicle. Near the centre they form communicating arches, not, however, with much regularity, since it frequently happens that three or more join to form one. Moreover, some few anastomosing branches run directly across to the opposite side. It thus occurs that in the centre of the follicles a non-vascular space frequently remains, which, however, is not larger than such as may be found between the capillaries in the periphery. One or more of these communicating capillary branches also frequently extend straight through the middle of the follicle.*

* For further information the reader is referred to F. Ernst, *Ueber die Anordnung der Blutgefässe in den Darmhäuten*, "On the Arrangement of the Vessels in the Walls of the Intestine." Zurich, 1851. His, in the *Zeitschrift für wissenschaftliche Zoologie*, Band xi., p. 416. Frey, in *idem*, Band xiii., p. 28.

The veins originate in the superficial plexus, especially from that situated at the base of the follicle, form short trunks which pursue a tortuous course, and partly coalesce with the veins of the villi, and partly open directly into a branch of the venous plexus lying upon the muscularis mucosæ.

Fig. 139.

Fig. 139. Vascular plexus of an intestinal follicle, seen in vertical section.

The bloodvessels of *Peyer's patches* present a similar arrangement to those of the follicles. The plexus lying subjacent to them is characterized by its richness; the larger trunks, both arterial and venous, completely surround the margin of the groups of follicles, and send numerous branches beneath the follicles. The venous plexus is especially distinguished from that of the other parts of the intestinal mucous membrane by the circumstance that, besides the vertically descending veins of the villi, numerous smaller and larger branches proceeding from the follicles unite at more or less oblique angles to form larger trunks, and thus cause a considerable alteration in the otherwise characteristic appearance of this plexus.

CHAPTER XVIII.

THE LIVER.

By EWALD HERING.

PROFESSOR OF PHYSIOLOGY IN THE JOSEPH ACADEMY OF VIENNA.

The liver, unlike other glands, elaborates its secretion not out of arterial blood, but from the venous blood of the vena porta. The very richly developed capillary network, into which the vena porta pours its contents, not only constitutes the starting-point of the hepatic vein, but also receives the blood from the hepatic artery, after it has flowed through a peculiar system of capillaries destined for the nutrition of vessels, gall-ducts, and nerves. The secreting cells of the liver are arranged in such a manner as to bring them into a much more intimate and extensive contact with the capillaries than is the case in other glands. Moreover, the number of the canals into which these cells pour their secretion is much greater than in any other gland in proportion to the number of the cells. Comparative anatomy shows that the liver should be placed near the tubular glands, although in the liver of the adult human being no tubular structure can be found, and even in the new-born infant it is barely indicated.

The Lobular Structure of the Liver.—The last offshoots of the arborescent hepatic vein are small, straight, or slightly bent vessels, which either leave the venous branches at a large acute angle or represent its forked end. They are called *central veins* (venæ intralobulares s. centrales) because each of them is embedded in the centre of the so-called lobule of the liver (lobulus s. acinus s. insula hepatis). Upon each central vein sits a small portion of the tissue of the liver, like a raspberry on its cone-shaped stem. These lobules, which correspond in number to the central veins, are packed together so closely as to be brought into immediate contact with each other; which gives them the appearance of being flattened wherever they press upon each other. In the liver of certain animals, the Pig for example, the lobules can easily be distinguished with the naked eye, and may even be isolated by maceration. On the surface of the Pig's liver four-, five-, or six-sided spaces will be seen, whose diameter averages 1.6 millimetres. The lobules of this liver are completely separated from each other by septa of connective tissue, which, in the outermost layer of the liver, are placed at right angles to its surface and give to the latter the aforementioned polygonal markings. In the human liver these septa of connective tissue are only very incompletely developed, so that throughout the greater part of its surface the substance of one lobule passes continuously into that of its neighbor.

The portal vein, which carries blood from the abdominal viscera to the liver, sends its branches throughout the latter organ in company with the hepatic duct (ductus hepaticus), the hepatic artery, and the hepatic nerves. All these canals are bound together and surrounded by fibrous connective tissue, which, under the title of Glisson's capsule (capsula Glissonii), also

gives shelter to the internal lymphatics of the liver. In the pig's liver the edges of the oblong, irregularly polyhedral lobules are blunt; hence, when the edges of three or four lobules come together, there will be left an *intermediate canal* (canalis interlobularis), into which small branches of the above-mentioned vessels push their way, while the connective tissue which surrounded them passes on continuously into that composing the septa of the lobules. The course of the small branches of the portal vein depends on the shape of the lobules, inasmuch as they run between the edges of the latter—that is to say, in the intermediate canals—and send their terminal branches into the septa of the lobules. From the fact that the small branches of the portal vein are situated only between the lobules, and at no point enter within them, they are called *intermediate veins* (venæ interlobulares). Now since all the intermediate canals of the pig's liver contain intermediate veins, the latter will in the main define the outlines of the lobules; then again, as the terminal branches of the intermediate veins are distributed throughout the septa, the surfaces likewise of the polyhedral lobules will be designated by them. At the same time the branches of the portal vein, which surround each lobule like a framework, do not anastomose with each other at any point. Finally, not only those most delicate branches of the portal vein, which lie between the edges of the lobules, but also those which are distributed over the walls of the septa, send numerous capillaries into all the lobules immediately adjoining them. These capillaries, which are distributed in the form of a network throughout the entire substance of every lobule, finally pour their blood into the central vein.

In the human liver the smaller branches of the portal vein also lie in similar canals between the edges of the lobules and are surrounded by connective tissue, but the latter is not distributed in the form of distinct septa between the lobules, but sends out only a few processes over the boundary surface between two contiguous lobules. Hence at the periphery of such a boundary surface the two lobules are separated by a little connective tissue—and even here the separation is only partial; the remaining portion, however, of the periphery and the entire central portion of the boundary surface is in fact only an imaginary one, for the masses of the two lobules run into each other without any intervening boundary. Into these incomplete septa of connective tissue run the short terminal branches of the intermediate veins, which lie in the intermediate canals; the edges and surfaces of a lobule of the human liver are therefore marked out, as they are in the Pig's liver, by the terminal ramifications of the branches of the portal vein, which approach the lobule from various directions, without however forming anastomoses at any part of its surface. From these ends of the portal vein is developed the capillary system of the lobules in exactly the same manner as in the Pig's liver, with this difference, however, that the capillary plexuses of two contiguous or adjacent lobules are in immediate communication with each other.

If we represent to ourselves the hepatic vein as a tree with countless branches, to whose last twigs—the central veins—the lobules of the liver are attached like oblong berries, we can then also imagine the portal vein as the trunk of another tree, entering the liver from the opposite direction, and sending its branches between the closely packed lobules, as a tree sends its roots into the clefts and fissures of a rocky soil.

The surface of the liver of an animal that is still alive appears of a uniform reddish brown, and shows no signs of its lobulated structure: the liver of a corpse is also in spots uniformly colored, but generally it has more or less of a marbled appearance, and seems to consist of two different substan-

ces, the one darker, of a rather reddish hue, the other lighter and bordering more on the yellow. This is more striking on the under surface of the liver, where the capsule is thinner, and on the surfaces of sections. At one time the darker substance appears in the form of small round spots, while the lighter substance forms a network in whose meshes those spots lie; at another the reverse is true—the darker substance forms a network whose meshes are filled with the lighter substance; and still again, the darker substance sometimes appears in the shape of convoluted bands, like the convolutions of the brain, the narrow intervening spaces being filled with the lighter substance. The lighter substance answers to the peripheral, the darker to the central portion of the lobules, and the difference in color is due to the fact that the peripheral portion of the lobules in the dead body is more bloodless than the central (Kiernan), and that moreover the pigment of the bile is deposited by preference in the central (Theile), while the fat seeks the peripheral portion of the lobules. On the surface of the liver the intermediate veins can often be recognized, even with the naked eye, as small straight or branching lines, or as mere points, in the midst of the lighter substance; more rarely the central veins can be seen in the middle of the dark substance. Sometimes each individual lobule can be recognized by a slight elevation or depression, which can be smoothed out or rendered more prominent by changing the tension of the surface, by means of pressure or by stretching.

The earlier belief in the complete lobular structure of the liver was combated by E. H. Weber* in opposition particularly to Kiernan.† Notwithstanding this, it is still advisable to consider the human liver, like that of the Pig, as made up of lobules, for it is only in this way that we can obtain a correct idea of the arrangement of the terminal branches of the portal vein, and of the distribution of the connective tissue.

THE STRUCTURE OF THE LOBULES OF THE LIVER.—The lobules of the human liver are irregularly polyhedral and usually oblong bodies, measuring 1 millimetre in their transverse, and 1–2 millim. in their long diameter. We distinguish in them a base, side surfaces, and summit. The base rests upon the wall of the small hepatic vein (vena sublobularis), from which the lobule receives its central vein direct. Those lobules whose central veins are not the lateral but the terminal branches of the hepatic vein, coalesce completely with each other in the neighborhood of their bases, so as to form a compound lobule (Theile). It also frequently happens that the central vein subdivides within the lobule, and that in harmony with this subdivision the latter, while retaining its single base, will have several distinct summits, separated by shallower or deeper furrows.

In cross-sections, that is, in such as traverse the central vein at right angles to its axis, the simple lobules appear of a rounded polygonal shape. In longitudinal sections, that is, in such as traverse the central vein lengthwise or are parallel to its axis, the lobules appear generally of an oblong shape; the compound ones are often like a leaf with scalloped edge, and might be compared to an oak leaf or to a portion of one. Wherever a central vein has been cut exactly crosswise or exactly lengthwise its distance from the nearest intermediate veins will be found to measure about 0.5 millim., that is, the semi-diameter of a lobule. Hence the distance traversed by the capillaries from the central to the intermediate veins is everywhere equally

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* *Programmata collecta*, Fasc. ii. Lips., 1851; and Müller's *Archiv*, Jahrgang 1843, S. 303.

† *The Anatomy and Physiology of the Liver. Philosophical Transactions*, 1833.

great. The lobules which lie immediately beneath the surface of the liver form an exception to this, for, being somewhat flattened at their upper extremity, their central vein approaches nearer to the surface (Kiernan).

The substance of a lobule of the liver consists essentially of two elements, the *liver cells* and the *capillaries.* In the same manner as the short trunk of a tree sends out branches on all sides at nearly a right angle to its axis, and at the top breaks up into radiating branches like a pencil, so the central vein gives off numerous capillaries from its entire surface. These latter seek the periphery of the lobule by the shortest route, and therefore follow in the main a radial course, but on the way they repeatedly make forked subdivisions. This accounts for the fact that these *radial* capillaries—as I shall call them—are placed as close to one another at the peripheral portion of the lobule as at the central. The diameter of these capillaries, when they are moderately distended, is about 0.01 millim., and they are separated from their nearest neighbors by a distance of about 0.015 millim. From the frequent intercommunication between these radial capillaries, through short transverse anastomoses, there is formed a very close capillary network with long meshes, whose long axis lies in the radial direction (within the lobule), while the short transverse axis corresponds to the distance between two radial capillaries. It is only at the periphery of the lobule, where the latter communicates uninterruptedly with its neighbor, that shorter and rounder meshes are found in the place of the oblong.

All the space which this omnipresent capillary network does not occupy is filled with liver cells. These we must imagine as small soft balls, which with a little force can be made to find room for themselves between two adjacent capillaries, so that when all the spaces between the capillaries are completely filled with these balls, the latter will not only become somewhat flattened by pressure upon each other, but they will also receive groove-like impressions on their surfaces from the capillary tubes with which they come in contact. Or again, we can represent to ourselves the totality of the closely packed polyhedral liver cells as one connected mass whose continuity is broken up by the many-meshed capillary network.

From what has been said above it follows that the internal arrangement of the lobules will vary considerably, according to the direction in which the section has been made. The radial arrangement of the capillaries and the oblong shape of their meshes can best be seen in those sections which traverse the central vein in its entire length. This gives to the lobule the appearance of a leaf whose central rib is here the central vein. On both sides the trunk of the central vein gives off capillaries which run like side ribs in a nearly parallel direction to the border of the leaf, and, at short intervals, are connected by transverse anastomoses; while the end of the central vein breaks up into a pencil of radiating capillaries. If the section is made at right angles to the central vein, then the latter appears as a circular opening, from which the capillaries radiate in all directions; but the capillary meshes, which lie in a radial direction, will rarely be seen in their full length, because the radial capillaries are usually not given off at an exact right angle with the trunk, but at a more or less acute angle. In consequence of this the capillary meshes appear shorter than they really are, for the section does not run exactly parallel with them. If the section is parallel to the long axis of the central vein, but has not been made through it, then a number of the radial capillaries will be cut exactly across, and the circular cross-sections of these capillaries will be seen in or near the median line of the section of the lobule, while on both sides of it and toward the summit of the lobule the radial capillaries will be cut at an acute angle to

their longitudinal axes—the angle growing more acute from the centre toward the periphery—and the entire capillary system will appear to have short meshes. If the section has been made in a direction at right angles to the central vein, without touching it, however, there will appear in the centre of the section the exact cross-sections of the radial capillaries, and the farther we go from it in all directions the more oblique will the sections of the capillaries appear, while at the periphery they will be arranged more irregularly.

From these simplest examples of sections it will be possible by analogy to explain the more complex, where the section has been made at any oblique angle whatsoever to the axis of the central vein, and where the latter is or is not included in the section. In every moderate-sized section of the liver there will be found examples of sections running in the greatest variety of directions, for the axes of the lobules themselves run in every conceivable direction. As a general result of these considerations it is to be remarked, that the instances where the radial capillary meshes are seen in their entire length must be comparatively rare, so that it would be quite easy to commit an error in relation to the arrangement of the capillaries.

The arrangement of the liver cells, inasmuch as it is determined by that of the capillaries, will likewise differ very much, according to the direction of the section. Since it is possible to pass from one radial capillary to several others without passing through more than one liver cell, therefore when two such neighboring capillaries are visible in the section throughout their entire length, there will be seen between them a single row of liver cells, which, toward the axis as well as toward the periphery of the lobule, are either separated from each other by transverse anastomoses of the radial capillaries, or anastomose themselves with neighboring rows of cells. The individual liver cells will therefore appear as more or less regular quadrangles, and the boundary line between any two of them will appear to cross directly from one capillary to the other. If the section is so thick that cells may be found lying above these two capillaries, the liver cells will appear—provided, of course, the section is at the same time sufficiently transparent—as five- or six-sided polygons, forming a continuous layer, which is broken only by the cross-sections of a few capillaries that come up from below to establish a communication with other radial capillaries, originally situated above the surface of the section. Around the cross-section of one of these communicating capillaries lie from five to seven liver cells in a circle. If the section passes through a number of radial capillaries exactly at right angles to their axes, the circular cross-sections of these will lie so close to one another that any two neighboring ones will be separated by only a single liver cell. In a few spots the short communicating capillaries will also be seen crossing from one radial capillary to another. With the exception of those cells which at the same time come in contact with a communicating capillary, the liver cells as a rule are in contact with only two capillaries, or perhaps one; more rarely with three.

In addition to these simplest appearances there will be found many of a more complicated nature, according to the place where the section is made and the direction which it takes. What has already been said will suffice to render intelligible why the liver cells are found to be arranged in apparently so varied a manner between the capillaries: at one time in long rows, which in some places communicate with each other like a net and form long meshes as in capillary networks; at another time, in the form of a close network, in whose small round meshes lie the cross-sections of the capillaries; at another time still, like an epithelium consisting of polygonal cells; or,

finally, arranged in some form which represents a combination of two of those just mentioned.

In the investigation of the minute structure of the lobules only those very thin sections will be found of service which do not materially exceed in thickness the largest diameter of a liver cell. At the same time the capillaries must be pretty well distended, either with blood or with a transparent, not too intensely colored injecting material. Care must also be taken in hardening the liver, for both in alcohol and in chromic acid the liver cells shrink, and so frequently become separated either entirely or in part from the neighboring capillaries, so that between them and the capillaries there will be left a free space. In the process of hardening, especially by means of chromic acid, the liver cells are very apt to fall out altogether from the capillary meshes and even to become dissolved. This occurrence does not by any means depend simply on the concentration of the hardening reagent and the length of time it is employed, but also on the condition of the liver at the time. Our examinations being limited to livers taken from the dead body, their condition will be found to vary to an extraordinary degree, according to the disease which preceded death, or the length of time that elapsed before making the autopsy. In the livers of certain animals, the Rabbit for instance, these unfavorable effects are not to be feared, not only because these livers can always be obtained in a fresh condition, but also because the cells of the latter do not easily become separated from the capillaries. The structure of the Rabbit's liver, however, is in some respects different: the number of the capillaries in proportion to the number of the liver cells is greater, and hence each liver cell comes in contact with three or four radial capillaries. We are therefore not permitted to apply, without certain limitations, the appearances of the Rabbit's liver—which I have described more minutely elsewhere *—to that of the human being; the Dog's liver resembles the human liver much more closely.

The description given here of the structure of the lobules of the liver differs materially from the descriptions hitherto given. All the more recent investigators, from E. H. Weber to Eberth, accept without a dissenting voice the existence of the so-called *hepatic cords* (Leberbalken); these cords are composed of one or more rows of cells and form a sort of network that intertwines with the capillary plexus. In the place of this commonly accepted view I have given my own individual interpretation, because the former appears to me to involve an impossibility, while the latter has already been confirmed by Kölliker. If the liver cells were really arranged in the form of cords or tubes, then any given mesh of the capillary network must represent the cross-section of an hepatic cord. The rows of cells, however, which led to the supposition of hepatic cords, lie parallel to the capillaries, in the long radial meshes of these latter, and are nothing more nor less than portions which have become isolated from the main body of the mass of liver cells by the section. If we imagine a large number of piles driven into the earth so closely together as to be separated from each other by only a distance equal to their own diameter, and imagine them at the same time to be connected together by a few short transverse beams, we shall then easily understand how, if all the intervening spaces of this framework be filled with any substance whatever, this will never assume the shape of a second framework interlocking with the first, but will simply represent a continuous mass that is traversed by anastomosing passages.

In Birds, Fishes, and Amphibia there exist, as I have shown † and as Eberth ‡ has also found independently of this, two interlocking networks. In the Snake's liver, for example, the liver cells are arranged like the epithelium cells of a tubular gland (see fig. 140). In the circular section of such a tube of hepatic cells, the latter are seen to the number of five or six, surrounding a small round opening—the cross-section of the

* *Sitzungsbericht der Wiener Akademie der Wissenschaften.* Dec. 6, 1866.
† *Sitzungsbericht der Wiener Akademie der Wissensch.* May 11, 1866.
‡ *Medicin. Centralblatt, December*, 1866, and Virchow's *Archiv*, 1867, Bd. 39, S. 70.

lumen of the gland-duct. Capillaries as well as glandular tubes form networks with small round meshes ; each mesh of the capillary network encloses the cross-section of an hepatic tube, and each mesh of the network of hepatic tubes surrounds the cross-section of a capillary. According to Von Biesiadecki * the human liver is similarly

Fig. 140.

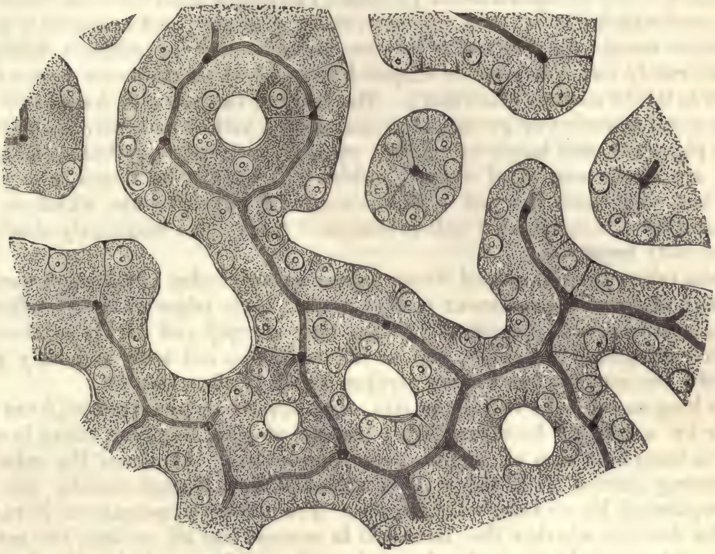

Fig. 140. From an injected Snake's liver. In the axis of the cords or tubes composed of liver cells run the dark threads of the material injected into the ductus hepaticus ; the empty spaces between the cells correspond to the blood capillaries.

constructed, in so far as thehepatic cords, when cut across, show a group of five or more cells, in the centre of which is an opening that answers to the gall duct. I myself have never seen anything of the kind, not even in the liver of the new-born infant, which, unlike the liver of the adult, shows in spots some resemblance to the livers of certain Amphibia, the Frog, for example ; this resemblance, however, consists simply in this, that in sections a round capillary mesh will frequently be seen enclosing three or four liver cells in the centre of which appears the narrow lumen of a gall duct.

It is the belief of some investigators that the cells of the human liver are surrounded in rows by a structureless membrana propria, and that the tubules which are thus formed—the so-called liver tubules—are connected together in the form of a network. In the walls of these tubules, according to E. Wagner,† round nuclei are found which measure $\frac{1}{400}$ ''' in diameter. In children, according to Beale,‡ the tubules can easily be separated from the wall of the capillary, while in adults it is either not practicable or else can only be done with great difficulty. From the description given above of the structure of the lobules it will be evident that such a membrana propria of the liver cells could only exist as a covering of the capillaries, so that what I have interpreted, partly from my own observations and partly from the views of other observers, to be simply the wall of the capillary would in fact consist of the latter together with the membrane of the tubules. Frey believes that this membrane encloses the perivascular lymph-spaces, in other words, that the lymph is contained between it and the wall of the capillary.

* *Sitzungsbericht der Wiener Akademie der Wissensch.* April 4, 1867.

† Wagner's *Archiv der Heilkunde*, 1860, I. Jahrgang, S. 251, where also the entire bibliography of this question is given.

‡ *On some points of the Anatomy of the Liver.* London, 1856.

THE LIVER CELLS.—The glandular cells of the human liver, discovered by Purkinje and Henle, come under our observation only in a dead condition· By passing the edge of a knife over the cut surface of the liver we can obtain a juice in which are suspended, together with other elements, numerous liver cells, either scattered or in groups. These appear as round, sometimes angular bodies, whose diameter (Kölliker) averages from 0.018 to 0.026 millim., and which consist of a colorless, finely granular, and apparently membraneless mass. In this are to be seen, though often not without difficulty, one or rarely two spherical or ellipsoidal nuclei whose diameter varies from 0.006 to 0.009 millim. (Kölliker). The body of the cell also frequently contains small granules or groups of granules of a yellow or brownish material (gall pigment), and larger or smaller strongly refractive globules (fat). If they are small several of these gloubles will usually be found in a single cell, but sometimes the cell contains only one large globule, which is surrounded by a thin layer of cell-substance. Such cells frequently attain an abnormally large size.

Cells taken from hardened livers appear as polyhedra of the most variable shapes; often with prominent peaked angles, their edges or their surfaces—when seen in profile—appearing at one time sharply and darkly outlined, at another irregular, indistinct, and as if torn. The cell body is darkly granulated ; the nucleus has a sharp outline which is often double.

So long as the cells remain in situ, they appear to be separated from each other by a delicate boundary line ; instead of this, however, there is often seen a fissure—a sign of commencing dissolution. At times the cells are intimately united with the wall of the capillary, though usually the two are separated by an intervening space. From these appearances it cannot yet be decided whether the liver cell is covered on all or only on certain sides with a membrane or hardened boundary layer, and also whether two contiguous cells are separated by a simple septum or by a glue-substance ; and this is all the more difficult from the fact that the livers of certain animals possess a very different arrangement. Thus for example the cells of the hardened Rabbit's liver can only be loosened with great difficulty from the capillaries, and the cracks and fissures, which so often appear in the livers of Man and many animals, are not to be found between the cells of the Rabbit's liver.

Besides the forms already described, liver cells are often found of a very different shape ; like scales, for instance, that are piled up on the capillaries, or like spindles of greater or less length, etc. etc.—concerning which anomalies nothing more definite can be mentioned here. Inasmuch as the living liver cell consists of a semi-fluid mass, it can be made artificially to assume the greatest variety of shapes, which it will then retain after it has become stiff or has been hardened.

THE GALL DUCTS OF THE LOBULES OF THE LIVER.—The intralobular (those running inside of the lobules) gall ducts of the human liver, termed also gall capillaries, have never yet been described ; I must therefore limit myself on this point to a statement of my own observations. These, however, only possess value when compared with what is already known concerning the intralobular gall ducts of the Mammalian liver.

In Mammals the injected gall ducts (figs. 141, 142) form a small-meshed network of delicate, mostly cylindrical canals of from 0.001 to 0.002 millim. in diameter, which run between the liver cells and enclose polygonal meshes, whose diameter equals that of a liver cell. The course which these canals almost always follow is, not along the borders, but between the boundary sur-

faces of two contiguous cells, dividing them (the surfaces) at one time into equal, at another into unequal halves. In certain animals, the Rabbit, for instance, this is almost exclusively the case, while in others, as for example the Dog, it happens in at least the majority of instances. But whenever the canals lie between the edges of several adjoining liver cells, it will be found that these edges do not in any way come in contact with a blood capillary, either at their ends or throughout their length. No gall duct can be found, therefore, which is not separated from the blood-vessels by intervening cell-substance. On the other hand, of the few cell edges which do not at some point come in contact with a blood-vessel, every one, with but rare exceptions, rests against a gall duct, and every boundary surface between two liver cells either carries in its median line a gall duct, or at least touches one with one of its sides. Whenever, therefore, in a well-injected lobule the boundary surface of two liver cells is seen in profile, that is to say, as a straight line, there will also be seen, with but rare exceptions, the cross-section of a gall duct, which will appear like a circular or oblong spot lying within that line, or, more rarely, at one end of it; or it may even appear, according to the position of the microscope, as a narrow staff, running parallel to that line, either by the side of, under, or over it.

Fig. 141.

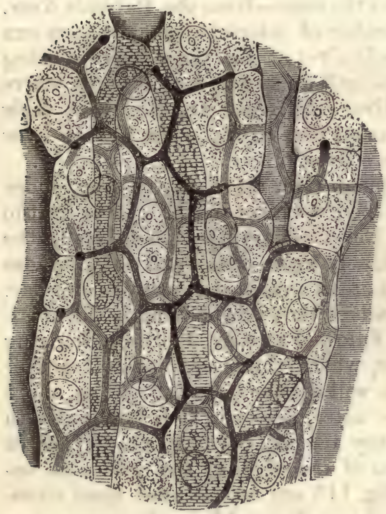

Fig 142.

Figs. 141 and 142. From an injected Rabbit's liver. The narrow reticulated gall capillaries are shaded with longitudinal lines, while the much broader blood capillaries are marked crosswise. Within the line of separation (septum) between two contiguous liver cells a dark spot may be seen, representing the cross-section of a gall capillary; in each liver cell, moreover, there may be seen either one or two nuclei.

If it be remembered now in what manner the liver cells are arranged between the capillaries, it will be easily understood how in thin sections, if only a single row of cells is visible between two radial capillaries, the gall ducts must appear, either as cross-sections, located within those transverse lines which run from one capillary to another and represent the profile views of boundary surfaces, or they must appear, when seen from the side, as ducts, more or less foreshortened, that run between the capillaries and are

nearly parallel to them. If in thin sections, however, the liver cells appear in the form of an epithelium, then the gall ducts will be seen as a network with polygonal meshes, each one of which encloses a liver cell. (Fig. 141.) If in a thin section the divided ends of the radial capillaries are seen, then the gall ducts will either appear as cross-sections—in which case they will be seen either in the course of those lines which, as profile views of the boundary surfaces of the cells, run from one capillary to another, or more rarely at those points where the boundary lines of several cells meet—or in the form of a network, and then every cross-section of a capillary will lie within a mesh of this net. (Fig. 142.)

This description is given from injected preparations. In the human liver, which at the very earliest can be examined only a few hours after death, the gall ducts of the lobules cannot be injected, owing to the rigidity which by that time will already have taken place in the liver cells. Nevertheless, they can be distinguished with a very strong magnifying power even when uninjected, and from such observations it has been ascertained that their arrangement is the same as in Mammals. After I had given an elaborate description of the gall passages of the Rabbit's liver, the description was accepted as applicable also to the human liver, whereas in point of fact it does not entirely hold good for the latter. In this respect the human liver can with much greater propriety be compared to the liver of the Dog, which differs in several respects—as I showed at the time—from the Rabbit's liver. In the Dog's liver by far the greater number of interlobular gall ducts run in the boundary surfaces of the liver cells; yet at the same time—a thing of rare occurrence in the Rabbit's liver—gall ducts are found lying where three, or, in extremely rare cases, four liver cells come together with their edges. This corresponds to the arrangement that exists in the human liver cells, but differs from that of the Rabbit's liver.

In very thin sections of a hardened human liver there may be seen, under favorable circumstances, a small, slit-shaped opening in the centre of the boundary line between two liver cells. The boundary line subdivides in the middle into two branches, which immediately unite again, and thus enclose the opening. Sometimes this opening is of an oval shape, or even circular. It is frequently possible to convince ourselves that this opening is the cross-section of a canal, for its outline can be followed to some depth by changing the focus of the microscope. Moreover, where three cells come together with their edges, the openings alluded to will appear either round, or, more commonly, triangular. In regard to the latter, however, it is impossible to decide with complete surety whether they are not, perhaps, simply spaces that have been created by the retraction of the edges of the cells—an occurrence of very great frequency. In fig. 143 are represented some cross-sections like these of gall ducts from the liver of a suckling; in very young children it is quite easy to demonstrate them.

In many human livers the gall ducts of the lobules may be followed with the same precision and completeness as in the best injected liver of a Mammal. It occasionally happens that the finely granular yellow coloring material of the liver cell is deposited exclusively in the immediate neighborhood of the gall ducts, while all the remaining mass of the cell is free from it. In that case the cross-sections of all the gall ducts will be surrounded by a yellow halo, which conveys the impression that the cell substance surrounding the gall duct must have imbibed gall.

In such livers it can be shown that, in by far the greater number of instances, the gall ducts run in the boundary surfaces, and only rarely between the edges of the cells. If the liver cells appear to be arranged

like an epithelium, the gall ducts will then be seen in the form of a network with pentagonal or hexagonal meshes, each one of which encloses a liver cell; in a word, the same appearances will be found again here which have already been described above concerning the Mammalian liver.

Fig. 143.

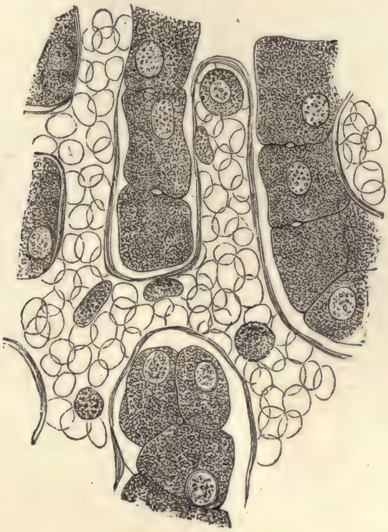

Fig. 143. From the liver of a three months old child, hardened in chromic acid. The single-nucleated liver cells are separated from the wall of the capillary by a narrow intervening space. The capillaries are filled with closely-packed colored blood-corpuscles together with a few colorless ones. A few elongated nuclei of the walls of the capillaries are also visible. Within the boundary line (septum) separating any two contiguous liver cells a small clear opening may be seen, representing the cross-section of a gall capillary; a similar opening may also be seen at the point where three liver cells come together with their angles (edges).

The gall ducts of the human liver, like those of the Rabbit, possess no membrana propria to separate them from the liver cells, but come in direct contact with the latter; and the layer immediately covering the gall duct—in case its isolation should ever be effected—may be designated as a thickened boundary layer of the cell substance, or as the cell membrane, or cuticula—all of which come to the same thing.

The intralobular gall ducts can easily be injected in the Rabbit by injecting Berlin blue dissolved in water into the ductus choledochus under a pressure of quicksilver of from twenty to thirty millimetres (MacGillavry), but care must be taken to bleed the animal to death, and to let the blood escape from the liver by making an opening in the lower vena cava. In other animals I have never yet succeeded in obtaining an injection that passed completely through the entire lobule. In the case of livers that are difficult to inject, the method of Chrzonszczewsky * will be found admirably adapted to the purpose; it consists in repeatedly injecting indigo carmine into the blood of the living animal, whereby the gall ducts become filled with the coloring material.

* Virchow's *Archiv*, 1866, Bd. 35, S. 153.

The true key to an understanding of the course pursued by the intralobular gall ducts lies, as I have already shown, in the fact that the ducts do not as a rule run along the edges but in the boundary walls of the liver cells. Inasmuch as my statements relative to this point have been verified already by Kölliker,* and in part also by Eberth,† I have made them the basis of the above description. By the method of direct injection the gall ducts of the lobules were first incompletely injected by Gerlach‡ in the Hog's liver, and then more completely injected in the Sheep's liver by Budge.§ The latter interpreted them not as intercellular passages, but as tubes provided with a nucleated membrana propria, on whose external surface the liver cells lay. MacGillavry adopted this view except as regards the existence of the nuclei, and represented the gall ducts of the lobules as a "capillary network," with its own special walls, and so intermingled with the network of capillary blood-vessels "that it was simply a matter of chance whether the tubes of the two systems touched each other, intertwined, or ran independently of each other." Chrzonszczewsky, Frey, and Irminger also share this view. According, however, to Andrejevic,‖ the intralobular gall ducts of the Rabbit "lie on the edges, while their points of bifurcation occur at the angles of the liver cells, so that their position corresponds exactly to that of the intercellular ducts of the parenchyma of a plant." Although Eberth has verified my view that the gall ducts run in the boundary surfaces of the liver cells, yet he gives an entirely different interpretation from mine to the whole structure of the Mammalian liver. According to him the ducts, in imperfectly injected livers of Mammals, "run in the axis of the anastomosing cords of liver cells and communicate with each other, but the side branches are either not at all, or only incompletely injected." The distance between these central gall tubules, that run along the edges of the cells, and the blood-vessels is equal to the diameter of a liver cell; "the side branches may either run between the edges of several contiguous liver cells or between the side surfaces of two opposite cells," and some of them, he says, end blind. He also gives two drawings of the Rabbit's liver, which answer to this description. Neither the description, however, nor the drawings seem to me to be suitable, for they both apply much more accurately to the liver of Amphibia than to that of the Rabbit. It is only in the newborn human offspring that I have hitherto met with anything similar. Blind terminations of gall ducts I have never yet seen in completely injected lobules of the Rabbit's liver. Biesiadecki gives the same description as Eberth of the intralobular gall ducts of the human being, only he locates them, as a rule, in the axis of the liver cords, where, in cross-sections of the latter, the duct usually appears, as we have already mentioned, in the form of a circular opening surrounded by five cells.

In gall ducts that have been injected with nitrate of silver and gelatine Eberth has seen a delicate doubly outlined membrane, and gives to it the name of membrana propria, by which is usually understood a membrane that surrounds glandular epithelium externally—a basement membrane, but not a cuticular formation like that, for instance, which is found in the cylindrical epithelium of the intestinal canal. While protesting against a membrane analogous in character to the wall of the blood capillaries—as the above investigators would make it out to be—I have nothing to say against a wall composed of the limiting membranes of the liver cells, although, in common with Eberth, I have never succeeded in isolating them, as MacGillavry and Chrzonszczewsky have done.

Kölliker's latest description corresponds in all material points with that given by me, and besides he has added this fact, that under certain circumstances the intralobular gall ducts of the rabbit can be seen in cross-section even in uninjected livers. He also expresses the hope that in a similar manner some one may succeed in seeing the gall ducts of the human liver.

THE PRINCIPAL GALL DUCTS.—The branching of the trunk of the gall ducts occurs at the same time and in the same locality with the portal vein and hepatic artery, so that, in cross-sections of the branches of the portal vein, there will always be found the cross-sections of one or more gall ducts.

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* *Handbuch der Gewebelehre*, V. Auflage, 1867.

† L. c. and Schultze's *Archiv f. mikros Anatomie*, III. Bd., S. 423.

‡ *Gewebelehre*, II. Auflage, 1854. S. 332.

§ Reichert und DuBois-Reymond, *Archiv f. Anat. u. Physiol.*, Jahrgang 1859, S. 642.

‖ *Sitzungsbericht der Wiener Akademie der Wissensch.*, 1861, Bd. 43, 1 Abtheil.

From these principal branches are given off finally the most delicate gall ducts which lie between the lobules. But there exist also collateral branches which are characterized, like the branches of the hepatic artery, by the formation of anastomoses. Already before entering the substance proper of the liver the hepatic duct and its principal branches give off superficial twigs, which break up into a network of anastomosing branches in the connective tissue that fills up the furrows of the liver. Connected with this network by anastomosis are other networks, which are located in Glisson's capsule, in the immediate vicinity of the principal gall ducts and branches of the portal vein, and communicate with the former. From all these networks twigs are sent into the parenchyma of the liver (Beale, Henle), where they finally break up into interlobular ducts. In various parts, moreover, of the surface of the liver there will be found gall ducts that send off branches into the neighboring connective tissue, where they also form anastomoses; in this way a few gall ducts find their way to the ligamentum triangulare sinistrum, and even to the diaphragm.

The principal gall ducts, down to those which measure 0.25 millim. in diameter, are provided with small simple or compound glands, which, according to Riess * and Kölliker, are embedded in the walls of the ducts. They consist of round or oblong vesicles, from 0.035 to 0.045 millim. in diameter, which either open directly into the gall duct, or several of them pour their contents into a single canal; this in its turn either opens directly into a gall duct, or unites with another similar canal to form a common outlet duct—an arrangement which gives to the whole gland the appearance of a cluster of grapes. This outlet duct often runs for quite a distance within the wall of the gall duct before opening into the calibre of the latter.

In the walls of the main trunk and larger branches there can be distinguished an inner layer or mucous membrane from an outer or fibrous coat. The latter contains smooth muscular fibres (Henle) and a few blood-vessels, while the inner coat is lined with a single layer of tall cylindrical epithelium cells, and is provided with a very close network of capillaries. The medium-sized ducts possess a lower epithelium, and their walls consist only of a single layer, which, according to Heidenhain,† also contains contractile fibre cells. The smallest gall ducts are distinguished only by their epithelium, which seems to lie free in the interlobular connective tissue, and consists of polyhedral cells that are frequently somewhat drawn out in the direction of the axis of the duct. The cuticula of the larger ducts, which consists of the transparent cell covers (Zelldeckeln) of the cylindrical epithelium, is also continued on—though constantly becoming thinner—over the lower cells of the smaller ducts, and gives to the lumen of the latter a peculiarly sharp outline (Eberth). The shape of the nuclei of the epithelium cells varies according to the shape of the cells themselves: they are of an oblong oval shape in the cylindrical cells of the larger ducts, round in the low epithelium cells of the smaller ducts, and oval in the smallest ducts, where the cells are somewhat drawn out in the direction of the axis of the duct.

In the free surface of the mucous membrane of the hepatic duct may be seen numerous shallow excavations, arranged without any degree of regularity. Similar excavations are to be found in all its branches, from the largest down to those which measure 0.5 millim. in diameter, only here they are arranged in two opposite rows along the course of the tube. These ex-

* Reichert und Dubois' *Archiv*, 1863, S. 473.

† *Studien des physiologischen Instituts zu Breslau*, IV. Heft, S. 241.

cavations correspond to the openings of the lateral gall ducts, or to the larger outlet passages of the glands; the small punctate pores, which are situated in or between the excavations, lead to the glands of the gall ducts.

The glands of the gall ducts possess no specific epithelium, but, like the ducts themselves into which they empty, they are lined with a cylindrical epithelium, and may therefore be considered as simple diverticula of the internal surface of the ducts, especially since, in those ducts that measure but 0.2 millim. in diameter, they actually appear in the form of small and sometimes very shallow depressions.

The finest gall ducts, which approach the same lobule of the liver from different sides, do not anastomose with one another; those, however, which accompany the same intermediate vein would seem occasionally to form anastomoses around it; but this point requires further investigation. These ducts pass on into the intralobular gall ducts, or gall capillaries, without any material diminution in their calibre. The liver cells come in immediate contact with the last epithelium cells of the ducts, and only occasionally do these epithelium cells seem to be somewhat enlarged at the spot where the one passes into the other. It often happens that, while the calibre of the gall duct is still bounded on one side by small epithelium cells, on the other side the large liver cells will already be visible. In fig. 144 there are representations of two spots in the periphery of a lobule of the liver, which show the transition from epithelium to liver cells. The liver was taken from a child three months old. In the injected livers of animals analogous appearances can be obtained, and at the same time the delicate thread, composed of the injected material, can be seen emerging from the epithelium-lined duct between the liver cells.

Fig. 144.

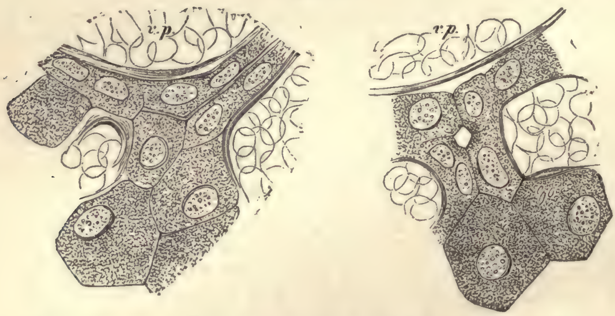

Fig. 144. From the liver of a three months old child, hardened in chromic acid. Both drawings represent fragments of a section made through the periphery of a lobule of the liver. The colored blood corpuscles of the blood-vessels will be recognized by their circular outlines. *v. p.* corresponds to an intermediate vein in whose immediate neighborhood lie the epithelium cells of gall ducts; these cells are uninterruptedly continuous with the much larger liver cells.

The absence of intervening elements between the small epithelium cells and the large liver cells has been one of the chief reasons why the transition from gall ducts to gall capillaries has for so long a time remained an obscure point. This transition consists simply in this, that the epithelium of the gall ducts suddenly changes its shape, while at the same time the calibre of the duct becomes only a trifle smaller.

In thin sections it is easy to demonstrate, under the microscope, the gall ducts and their epithelium. To see the branching of the gall ducts and

their networks, they must be injected with a colored material: it must be remembered, however, that, in a liver taken from a dead body, the epithelium is very easily destroyed by the injection. The glands of the gall ducts can best be examined under the microscope after the ducts themselves have been injected with feebly colored gelatine.

The *gall bladder* is lined with a mucous membrane, which is thrown into numerous intercrossing ridges and a few low conical eminences. It is provided with a very close capillary network, like that of the intestinal mucous membrane with its villi, and is lined with an epithelium of very tall cylindrical cells, which carry on their free surface a thickened striated rim, similar to that which is seen in the cylindrical cells of the intestinal mucous membrane (Virchow*). The layer of interlacing bands of smooth muscular fibres, which is traversed by bundles of connective tissue and by broad-meshed capillaries, is described by Henle as a part of the mucous membrane. On the outer side of this follows still another layer of connective tissue, and then comes finally the peritoneum on the free surface of the gall bladder. The larger vessels of the gall bladder, and especially the veins, are very numerous. With every artery there are two accompanying veins (Beale), and every two such parallel veins are united by numerous anastomoses which bridge over the intervening artery; this gives to the whole venous system a strong resemblance to lymph vessels. On the free surface of the gall bladder there are found numerous large subserous lymph vessels; fine lymph vessels have not been demonstrated either here or in any of the other layers of the bladder. According to Luschka,† the wall of the bladder contains a few small mucous glands, like those of the ductus cysticus, choledochus, and hepaticus. The ductus cysticus, in conformity with the structure of its walls, should be considered as a continuation of the gall bladder.

E. H. Weber described the net-shaped, anastomosing gall ducts in the fossa transversa as vasa aberrantia, because he interpreted them as ducts of a corresponding portion of liver parenchyma which had failed to reach its full development. He gave the same interpretation to the other ducts which are to be found outside of the liver substance proper. Theile,‡ however, in consequence of his discovery of the glands of the gall ducts, interpreted the whole mass of ducts, that occur in the transverse furrow, as net-shaped anastomosing mucous glands, and applied the same interpretation also to the network of gall ducts in Glisson's capsule. Those gall ducts, however, which are to be found in the ligamentum triangulare sinistrum (Ferrein, Kiernan), in the connective tissue membrane which sometimes bridges over the vena cava and serves to bind Spigel's lobule to the right lobule of the liver (Kiernan, Theile), in the fossa pro vena umbilicali (Kiernan, Weber), and along the border of the gall bladder, Theile considers as gall ducts which have lost their appropriate lobules through atrophy of the same. That this view is justifiable in relation to a portion of the ducts may be inferred from the fact that in old men the sharp edge of the liver becomes converted through atrophy into a mass of connective tissue, in which are found numerous gall ducts, but no longer any liver cells; this view is also corroborated by the fact that a similar condition of things may be seen in the so-called contracted livers, in the spot where the pressure of the contracting band has produced a callous furrow along the surface of the liver.

At a later date the glands and networks of the gall ducts were described by Wedl § and Beale, though not so thoroughly as it has been done recently by Henle ‖ and Riess; the last-named writer lays great stress on this point: that the glands, by being

* Virchow's *Archiv*, 1857, XI. Bd., S.574.

† Henle und Pfeuffer's *Zeitschr. f. ration. Medicin.* 1858, IV. Bd., S. 189.

‡ Rud. Wagner's *Handwörterbuch der Physiologie*, II. Bd., 1844.

§ *Sitzungsbericht der Wiener Akad. d. Wissensch.*, Dec. 12, 1850, V. Bd., S. 481.

‖ *Handbuch der Anatomie*, II. Bd., Eingeweidelehre, 1866.

embedded in the walls of the ducts, must be looked upon, not as "appendices of the ducts as a whole, but only as appendices of their calibre."

The Blood-Vessels of the Liver.—The liver contains two systems of blood capillaries, that of the vena porta and that of the hepatic artery. The former, already described above, is characterized by the breadth of its capillaries and the smallness of its meshes, while the latter possesses narrow capillaries and broad meshes; the former is confined to the inside of the lobules of the liver, while the latter is distributed to all the tissues that lie outside of the lobules. Both are connected to such an extent that the blood from that system of capillaries which is fed by the hepatic artery is poured in part directly, in part indirectly, into the system which is fed by the vena porta, so that finally the central veins of the lobules carry off not only the blood from the vena porta, but that also from the hepatic artery.

The vena porta and hepatic artery ramify throughout the liver in company with each other, but the hepatic vein subdivides separately from the other two; the branches of the vena porta are surrounded by the loose connective tissue of Glisson's capsule, while the hepatic veins are firmly attached to the substance proper of the liver by a scanty connective tissue. The intermediate and central veins are either the terminal branches of the vena porta or hepatic vein, or they are the direct lateral branches of some of their larger trunks. The large twigs, however, of the portal and hepatic veins give off no intermediate or central veins directly to the lobules which are in their immediate neighborhood; these last receive their intermediate and central veins by circuitous routes from the larger vessels. A difference, therefore, exists here between the portal and hepatic veins, inasmuch as the latter sends off, even from its relatively large branches, central veins directly to neighboring lobules. Hence, on the internal surface of such hepatic veins, in addition to the larger openings, very fine pores will be recognized which lead into the central veins. In those cases where small hepatic veins give off on all sides central veins (venæ sublobulares), these latter will be found to enter the neighboring lobules by way of their bases; with the larger veins, however, this is not often the case, as then the lobules usually present their side surfaces or summits to the vessel.

At no point in their course do the branches of the portal vein anastomose with one another, and where two intermediate veins approach each other from opposite directions, running at the same time between the same lobules, these will never unite, but will both break up into capillaries. This is equally true of the small branches of the hepatic vein. The portal vein, moreover, and the hepatic vein do not form a junction at any point except through the intervention of their capillaries.

The branches of the hepatic artery anastomose with each other and form a network with large meshes, which in part is woven round the vessels that lie in Glisson's capsule (rami vasculares arteriosi), in part surrounds the larger veins, and in part is distributed throughout the external capsule (rami capsulares arteriosi); this peculiar distribution must have an important influence on the mechanism of the current of the blood. From this arterial network capillaries are given off which, in comparison with the capillaries of the portal vein, are very narrow; they form a network with long and very broad meshes, except in the vicinity of the larger gall ducts, where the meshes are quite small. These capillaries accompany the larger vessels and penetrate with Glisson's capsule between the lobules; they are also distributed throughout the external capsule of the liver. The blood from these capillaries flows partly, as Ferrein discovered, into small veins—

the so-called central roots of the portal vein, which usually accompany an arterial branch in pairs (Beale), and pour their contents into small branches of the portal vein—and partly into the capillaries of the portal vein direct, which happens wherever the two capillary networks lie in close proximity, as, for instance, in the external capsule and the interlobular connective tissue. The former course is followed in those places where rather thick layers of connective tissue separate the two capillary systems, as, for instance, in the neighborhood of the larger blood and gall vessels.

Small branches of the portal vein and hepatic artery approach the external capsule in company with one another, by way of the intermediate canals of those lobules which lie nearest the surface of the liver. The former very soon break up into their terminal branches; they correspond to the intermediate veins, and supply the lobules of the liver with blood from the side which is turned toward the external capsule. The latter, on reaching the external capsule, at once break up into a number of branches, which are often arranged in the form of a star; these follow to a certain extent a tortuous course and unite farther on with neighboring branches, thereby forming a broad-meshed arterial network, which is connected by anastomosis with the arteriæ mammaria, phrenica, and suprarenalis.

The capillary network of the lobules of the liver can be injected from the portal vein, from the hepatic vein, and from the hepatic artery; while the capillary network of the hepatic artery can only be injected through the latter.

A very accurate description of the blood-vessels of the liver is given by Theile, who has also already described the arterial network in both Glisson's and the external capsule under the name of plexus arteriosus. I find, however, no mention made by him of the fact that the larger hepatic veins are surrounded by an arterial network. Johann Müller assumed that there was a direct passage between the delicate arteries, that penetrate between the lobules, and the capillary network of the portal vein. Theile found, however, that these arterial branches, which accompany the intermediate veins, also break up into capillaries, a fact which may very easily be demonstrated in the Hog's liver. Theile, Henle, and Kölliker assumed, with Johann Müller, the existence of special rami venosi capsulares, which, like the above-mentioned inner roots of the portal vein, transmit the blood from the venous capillaries of the external capsule of the liver to the branches of the portal vein.

THE LYMPH VESSELS OF THE LIVER.—The Human liver is very rich in lymph vessels, which in this organ, as everywhere else, follow the course o. the connective tissue. In other respects also the lymph vessels of the liver are not to be distinguished from those of other organs. The capillaries, as well as the larger vessels, are constantly forming anastomoses with one another. Numerous large trunks, provided with valves, carry off the lymph, partly by way of the hilus of the liver, partly by way of the external capsule, where they exist in large numbers, especially in the neighborhood of the ligamentum suspensorium.

The *superficial lymph vessels*—those situated in the external capsule—form with their capillaries and finer trunks an extremely compact network, whose meshes are much closer than those of the capillary network formed by the breaking up of the hepatic arteries in the external capsule. Each of these capillary networks runs its course entirely independent of the other. The larger branches usually accompany the arteries, which lie in the external capsule, in pairs, and every two such parallel vessels are at certain spots united by transverse bridges.

The *deep lymph vessels* of the liver—those which lie in Glisson's capsule—are likewise very numerous; they inosculate very extensively and form a

capillary network, whose meshes, however, do not seem to be so small as those of the network in the external capsule. Surrounding the transverse section of a branch of the portal vein, measuring 0.8 millim. in diameter, I once counted about twenty transverse sections of lymph vessels. The deep lymph vessels anastomose on the surface of the liver with the superficial, and numerous small trunks approach the external capsule from below in company with the small branches of the portal vein and capsular branches of the hepatic arteries.

The demonstration of the microscopic lymph vessels of the Human liver is a comparatively easy task. Although they may be injected with colored substances, either by inserting the nozzle of the syringe into the connective tissue in any part of the liver, or by injecting the gall passages from which, under excessive pressure, the material injected will easily escape by extravasation, nevertheless these methods—which depend on good luck for success—frequently furnish indistinct specimens. The injection of the lymphatic trunks according to Teichmann's method will on the contrary furnish clear and trustworthy specimens. With the needle a small opening should be made in as small a lymph vessel as possible either of the external capsule or of the hilus of the liver, and into this opening a small canula must be inserted in such a manner that the injecting fluid will have to flow in the same direction as that pursued by the lymph during life. After one or several larger lymph trunks have been filled, they are to be closed by clamps at their proximal ends; the fluid thus dammed up will then commence to flow backwards into the small peripheral lymph vessels, which are provided with only imperfect valves. In this way, owing to the numerous anastomoses between the lymph vessels, quite large tracts may be injected, not only of the superficial but also of the deeper system of lymph vessels. When the long and slightly conical canulæ are in position, I am not in the habit of placing ligatures around them, but simply hold them tightly with my hand during the short time occupied by the injection, and I find that this mode of closure is amply sufficient; for a strong pressure or one of long duration must not be used in the injection if we wish to obtain clear specimens. All other methods are far inferior to this in point of trustworthiness.

The drawings of the lymph vessels of the liver, which Teichmann has published, do not give an entirely satisfactory representation of these vessels, for the separate portions of the network are very irregularly filled, so that the lymph vessels everywhere appear swollen into knots. A good injection, made under moderate pressure and with a material that flows readily, will display, especially in the external capsule of the liver, a much more uniform formation of the lymph vessels.

Kölliker found that in animals the hepatic veins were also surrounded by lymph vessels—a condition of things which has not yet been proven to exist in the Human liver.

According to MacGillavry the deep lymph vessels of the Dog's liver communicate directly with crevices (spaces not provided with special walls) in the connective tissue of Glisson's capsule. This investigator injected either a watery or a gelatinous solution of Berlin blue into the large lymph vessels of the hilus of the liver in the direction against the valves: he also made injections by thrusting the point of the syringe into the connective tissue. Both methods require strong pressure, and therefore necessitate an enormous dilatation of the lymph vessels, which, of course, is frequently accompanied by extravasations. Since, moreover, a lymph vessel, especially if it has been distorted by excessive pressure in the process of injection, can be distinguished from a crevice in the connective tissue, that has been produced by extravasation, only by demonstrating the characteristic epithelial markings, I hold that MacGillavry's view is not proven by the facts. The results of my own injections of the lymph vessels of the Human liver, which were performed according to the above-described methods, also invariably conflicted with his view.

According to Biesiadecki, all the capillaries of a lobule of the Human liver float, as

it were, in lymph spaces—which in shape and arrangement are entirely like the capillaries, with the exception that they are somewhat broader, so as to contain the latter. Hence the liver cells must everywhere be separated from the capillaries by a space that is filled with lymph. These so-called *perivascular lymph spaces* were first described by MacGillavry * in the Dog's liver: at a later period Frey and Irminger † described them in the livers of the Rabbit and other Mammalia. According to a precursory description by Kisselew,‡ these perivascular lymph spaces in the liver of the Dog and Pig possess the epithelium that is characteristic of lymph vessels, and are therefore perivascular lymph vessels. All the above-named investigators are agreed that these intralobular stand in direct communication with those interlobular lymph vessels which are situated in the connective tissue of Glisson's capsule.

I hold that the existence of such perivascular lymph vessels has not been fully proven, although it is an easy matter in the Human and Dog's liver to demonstrate perivascular spaces, and although these can be to a limited extent injected. The cells of the Human and Dog's liver, as I have already mentioned, easily become detached from the capillaries; this is especially true of specimens preserved in alcohol, in which fluid not only the cells but also the capillaries become shrunken, so that relatively broad and empty spaces are produced between the two, which are clearly of artificial origin. These spaces may be found of almost any breadth, according to the method of hardening employed. In the Human liver, moreover, it must also be remembered that the degree of shrinking will vary according to the nature of the previous disease and the amount of water it may have superinduced in the liver cells. If, as is the case with the Human and Dog's liver, the connection between the liver cells and blood capillaries be rather loose, it will then be possible, especially in disturbances of the circulation, for a layer of fluid to accumulate between the two, that will still further assist the effects of the hardening process in bringing about a complete separation of the cells from the capillaries. All this, however, does not justify our assuming the existence of perivascular lymph vessels. We would have just as much right to infer that, because a certain amount of fluid lies between the bundles of fibrillated connective tissue, therefore each of these bundles of connective tissue is contained within a lymph vessel. The results of injections also prove nothing, for the so-called perivascular lymph vessels may have been injected only through extravasation. The injecting material must of course force its way somewhere, if it be driven forward with excessive pressure; and what is more natural than that it should separate the loosely-connected liver cells from the blood capillaries and push its way between the two? In the Rabbit this separation does not take place, and hence it is that perivascular lymph vessels cannot be injected in the liver of this animal: under excessive pressure the injecting material always forces its way here into the blood capillaries and fills them. The statement that in the Rabbit's liver perivascular lymph vessels can be injected is incorrect; and in the circumstance, that no such spaces can be demonstrated in the liver of this one animal, I find a very weighty reason against the belief that they exist in the livers of other animals.

The Connective Tissue of the Liver.—The liver possesses a superficial and deep fibrillated connective tissue. The former constitutes the external capsule of the liver, the latter Glisson's capsule. The external capsule of the liver is a membrane that varies very much in thickness in different parts of the surface, although as a rule it is so thin that the substance of the liver can be distinctly seen through it. Wherever the liver is invested with the so-called peritoneal covering, it will be found possible in certain spots, especially after maceration, to separate the external capsule into an upper ("serous") and a lower ("fibrous") layer (Theile). The deep connective tissue surrounds the larger vessels and constitutes the incomplete septa of the lobules. Bundles of connective tissue do not enter into the interior of the lobules of a normal liver, but a few scattering fibres of intralobular connective tissue may be found there; of these a part may be seen—especially in the peripheral portion of the lobule—lying upon the capillaries, while the

* *Sitzungsbericht der Wiener Akademie d. Wissensch.*, April 28, 1864.
† *Zeitschrift für wissenschaftliche Zoologie*, 1866, 16 Bd., S. 208.
‡ *Medicinisches Centralblatt*, Feb. 20, 1869.

others lie stretched out in straight or branching threads between the capillaries, and therefore possess more or less the aspect of reticulated connective tissue. The nucleated elements, that are occasionally to be seen lying on the outside of the capillaries, are commonly interpreted as connective-tissue corpuscles. The intralobular connective tissue can be demonstrated most successfully in livers that have been properly hardened in chromic acid. If very thin sections are made from these, the liver cells will be found to have dropped out of themselves along the borders and from the thinnest portions of the section, thereby leaving the capillaries and the above-mentioned fibres completely isolated. Thicker sections will have to be agitated for some time in the hardening fluid, or—if they are very thick—the cells may be displaced by pencilling.

His * considers the extremely fine, striated, or retiform markings, that are frequently seen on the walls of well-isolated capillaries, as the adventitia capillaris, but has not found any connective tissue corpuscles in it. He was also the first to call attention to the delicate cords, which are sometimes seen stretched across the empty capillary meshes from one capillary to another, and are frequently attached to the wall of the capillary by a funnel-shaped expansion. Henle and Kölliker confirm this last discovery, yet the latter is inclined to look upon these small cords as capillaries which are in progress either of development or of atrophy. According to the same authority there is to be found, in addition to the stellate connective-tissue corpuscles, only an extremely small amount of amorphous connective substance. E. Wagner † was the first to note the presence of connective-tissue corpuscles inside of the lobules—a fact which was afterwards confirmed by Engel-Reimers, ‡ Kölliker, and Förster. § Henle, however, disputes the presence of the connective-tissue corpuscles, but admits that all the capillaries are accompanied by threads of connective tissue which are thick enough to appear like dark granules when seen in transverse section. All these differences of opinion may be explained chiefly by the fact that it was not in all cases accurately noted whether the part under observation was the central or the peripheral portion of the lobule, whether the liver were entirely normal or not, and whether it was fresh or old. The spindle-shaped liver cells, which are not of rare occurrence, may have been mistaken at times for connective-tissue corpuscles.

The deep connective tissue of the Human liver presents such variations in its appearances that, unless a person has examined an enormous amount of material, it would be difficult to determine what is the normal condition of things and what is not. In grown-up Dogs the following may be considered the normal condition of the deep connective tissue: the fibrillated interlobular connective tissue sends only a few thin and but feebly striated bundles into the outermost layer of the lobules. These bands at once break up into smaller, apparently homogeneous cords which—if the liver cells have already been removed—appear to be stretched between the capillaries. These cords may also frequently be found stretched across the capillary meshes of almost any portion of the lobule. At one time we shall find but a single cord stretching from one capillary to the other; at another time the cord will subdivide midway, each branch of the fork attaching itself to the nearest capillary; then again several cords will start from the periphery of a capillary mesh, and, as they approach the centre, they will frequently subdivide and anastomose with one another so as to form in some instances a beautiful network of extremely fine threads, which resembles in every respect reticulated connective tissue. This connective tissue possesses no nuclei. Inasmuch as not even a trace of a membrana propria is anywhere to be found connected with the liver cells, this scanty reticulated connective tissue, together with the liver cells and blood capillaries, are therefore the only formed elements clearly proven to exist in the lobules.

THE NERVES OF THE LIVER.—The goodly number of nerves, that enter the hilus of the liver and follow the vessels of Glisson's capsule in all their ramifications, contain besides the non-medullated fibres only a few medul-

* *Zeitschrift für wissenschaftliche Zoologie*, 1860, X. Bd., S. 340.
† *Oestreichische Zeitschrift für praktische Heilkunde*, March 29, 1861.
‡ *Explic. micr. de tel. hepat. conjunct.* Berol, 1860.
§ Kölliker, *Handbuch der Gewebelehre*, V. Aufl., S. 438.

lated, which in the smaller bundles are constantly diminishing in number. The finest bundles contain only non-medullated fibres. All demonstrable nerves lie outside of the lobules; on the inside of the latter I have not been able to find any. Since here—as one can easily prove in very fine sections of a hardened liver—there are no fibres or other visible elements to be seen besides the liver cells, capillaries, and the scanty connective tissue described above, we must assume that, if nerve fibres penetrate into the interior of the lobules, they must be of extraordinary delicacy.

In a short preliminary communication Pflüger reports that he has reached entirely different results by treatment of the liver with perosmic acid. I also have used this reagent considerably but have not yet seen anything similar to what Pflüger describes. The preceding detailed description will, I trust, throw light on the cause of this contradiction.

CHAPTER XIX.

LARYNX AND TRACHEA.

By E. VERSON.

A. Larynx.

Framework.—The changes in form, which the modulation of the voice requires of the larynx as a tone-producing apparatus, are effected exclusively by the voluntary muscles, for whose effectual working, however, firm points of support are needed. These are afforded by the cartilaginous framework, whose peculiar shape and construction render a variety of motions possible, which will be found to differ in the several classes of animals according to the requirements of their vocal capacities.

In the primitive larynx of the Proteus there is found on both sides simply a cartilaginous band; but as we rise through the higher ranks of Mammals there is formed from this—according to Henle—by scission, transverse growth, and partly by resorption, that complicated structure which in form and capacity is found to be so perfect in the Human being.

While in the lower classes of animals there is but a single cartilaginous plate on either side of the larynx, in the highest Mammals this becomes subdivided into seven or more separate pieces, firmly held together by suitable bands. Hence our description of the framework of the larynx must comprise not only the cartilaginous portions but also the bands that connect them together.

The cartilages of the Human larynx belong partly to the hyaline and partly to the fibrous variety, and in youth are subject to pretty active nutritive changes, which are carried on by their own vessels and regulated by their own nerves. Thus in certain spots the perichondrium sends processes into the substance of the cartilage which consist of delicate connective tissue with numerous spindle-shaped cells; among these larger and smaller vessels, together with a few nerve fibres, can be distinctly recognized. In the adult Human being the direct communication between the cartilages and the vessels of the perichondrium ceases, or at least becomes very much restricted.

With advancing age the hyaline cartilages undergo ossification; in most cases this first appears after the fortieth year, although exceptionally it may occur much earlier, even at the twentieth year. The process begins with a simple deposit of lime salts in the basis substance and spreads with tolerable uniformity outwards from the so-called bony nuclei. The limit, however, of this ossifying region is not sharply marked. At first scattering, punctate deposits take place in the basis substance of the cartilage; these grow constantly thicker and finally unite with the uniformly calcified basis substance. Near the limit of ossification the cartilage cells still appear unchanged, but at a greater distance from it, where the substance has been calcified for a long time, they will be found already to possess numerous outrunners, which give to them a perfectly stellate shape, and render it impossible to distinguish them from the ordinary bone corpuscles. In the

fibro-cartilages, as a rule, ossification does not take place even with advancing age; the only exception to this is the arytenoid cartilage of the Dog, which occasionally undergoes ossification.

To the purely fibro-cartilages belong the epiglottis, the cartilages of Santorini and Wrisberg, and the not always present sesamoid cartilages. Among the purely hyaline are reckoned the thyroid and cricoid cartilages and the corpusculum triticeum, whereas the arytenoid cartilage is partly hyaline and partly fibrous.

The cartilage of the *epiglottis* appears to possess on its posterior (inferior) surface numerous pits and holes, which often pass entirely through its substance, and then usually afford passage to vessels and smaller nerve trunks. The shallower pits serve as a receptacle for fat cells or acinous glands—which last are only found on the posterior surface of the epiglottis. The perichondrium of course penetrates into all the pits and holes of the cartilage. The epiglottis becomes ossified only in Reptiles and Birds, in which animals it is more firmly united to the thyroid cartilage.

The *thyroid cartilage* is generally hyaline in structure, but in it there are a few spots in which fibres also may be seen between the cartilage cells. This is the case at the borders from which the elastic bands run to the hyoid bone and cricoid cartilage; but it is even truer of the anterior edge of the thyroid cartilage, at the height of the true vocal chords, whose outermost fibres penetrate deeply into the cartilage and subdivide it, to a certain extent, into three sections—a median, situated between the vocal chords (lamina mediana, Halbertsma), and two lateral. In the new-born child the arrangement is different; for while there is also here a subdivision into three parts, it simply amounts to this, that the closely packed cartilage cells of the middle section terminate on both sides in an outwardly concave line, beyond which the cells appear fewer in number, though larger. An actual trisection of the thyroid cartilage occurs only in Birds. Finally, even in the centre of the substance of young thyroid cartilages, bands of fibres are sometimes found, either alone or as the support of vessels.

As to the *cartilages of Wrisberg*, it is known that they sometimes become subdivided into three or more rounded nodules, arranged either one on top of the other, or in a row. At the same time the perichondrium of the several nodules breaks up into radiating fibres, which interlace in different directions and so give rise to interspaces in which acinous glands are embedded.

The *Cartilago Santorini* (corniculata) appears to be separated from the arytenoid cartilage only by a prolongation of the perichondrium, that differs from the rest of the perichondrium in being somewhat softer and containing a few scattering cartilage cells. In texture it usually appears to be fibrous, but sometimes a hyaline kernel is found concealed in the centre of the fibrous shell.

The actual body of the *arytenoid cartilage* possesses a purely hyaline structure. Its peripheral portions, however, are often fibrous in character, which is invariably true of the processus vocalis and the summit of the pyramid. It is a remarkable circumstance that in the Dog the formation of cartilage may extend from the arytenoid cartilage into both vocal chords. In such cases these latter contain in their substance a lamella of fibro-cartilage, which extends pretty far forwards, and is connected with the combined Santorinian, Wrisbergian, and arytenoid cartilages.

The different cartilages are bound together either by bands or joints, according as mobility is required, either with a certain amount of play or with fixed points of support. The bands are connected on all sides with the

surrounding tissues. They are composed chiefly of elastic tissue with a few fibres of connective tissue, and—in childhood—very numerous spindle-shaped cells. In the neighborhood, moreover, of their attachment to the cartilages, they generally contain in their substance cartilage cells, which grow more numerous the nearer we approach to the point of attachment, until finally they become merged in the true cartilage.

Articular connections exist between the cricoid and arytenoid cartilages; also between the cricoid and thyroid cartilages.

The surfaces of the crico-arytenoid joint are hyaline, and are characterized simply by a closer arrangement of the somewhat smaller cartilage cells which lie with their long axes parallel to the surface of the joint. That portion of the articular surface which belongs to the cricoid cartilage receives from the capsule, at the point where the latter joins it, a few fibres; these radiate through the surface of the joint, but soon become lost as they approach its centre. The capsule, on the other hand, contains in the neighborhood of its attachments cartilage cells which penetrate into it from the cartilage. From behind and outwards an intermediate piece insinuates itself into the joint; it starts with a broad base from the capsule and terminates with sharp edges in the midst of the cavity of the joint. Its texture consists chiefly of a dense and firm fibrous tissue containing a few large cartilage cells, but is not covered with epithelium as is the rest of the internal surface of the articular capsule.

The capsule of the crico-thyroid articulation consists principally of connective tissue, which is continued over the articular surfacc of the cricoid cartilage, traversing it throughout its entire breadth. Cartilage cells are scattered throughout the tissue of the entire capsule. The bands that give strength to this joint appear also to be comparatively poor in elastic tissue.

Soft Parts.—The *epiglottis* is covered by a mucous membrane which, at the free extremity of the epiglottis, is very thin and is attached to the perichondrium by a tense and scanty connective tissue. The mucous membrane contains numerous elastic fibres which run in a longitudinal direction: in their meshes lie numerous round bodies which possess one or more nuclei each, and are more closely packed together along the sides of the vessels of the mucous membrane and immediately beneath its epithelium. In transverse sections of the posterior side of the epiglottis the free surface of the mucous membrane seems to be limited toward the epithelium by a sharp straight line, whereas transverse sections of its anterior side show wavy border outlines with papillæ, 0.7–0.18 millim. in length, that project into the epithelium; the larger of these papillæ sometimes break up into two or three extremities, each containing beautiful vascular loops. Toward the entrance to the larynx the mucous membrane becomes thicker, and at the same time stands out in more decided contrast with the loose submucous tissue; from this point down it varies from about 0.1–0.15 millim. in diameter. Only on the upper vocal chord is it sometimes found of a considerable thickness.

The epithelium on the anterior surface of the epiglottis consists of a thick layer of pavement cells, measuring 0.2–0.3 millim. in thickness. On the posterior surface it is much thinner, measuring only 0.06–0.1 millim. in thickness, and its deepest layer consists of delicate cylindrical cells, arranged side by side, like a palisade; above these lie cells which are more rounded or polygonal in shape, and therefore constitute a sort of stratum Malpighii beneath the flattened cells of the horny layer. On approaching the prominence of the epiglottis, while the basilar cylindrical cells are con-

tinued on, the other layers of cells above them gradually diminish in thickness and finally disappear altogether, leaving behind the basilar cells, which in the mean time have grown longer and have become surmounted with cilia, 0.005 millim. in height. Between the bases of these ciliated cells numerous

Fig. 145.

Fig. 145. Epithelium of the posterior surface of the epiglottis, with one of the bud-like structures. *a*, transverse section of the central canal.

round and oval cells will be found, and the new epithelial covering may now measure 0.15 millim. or more in height.

The transition from the epithelial formation of the anterior to that of the posterior side of the epiglottis takes place in this wise: the pavement epithelium of the anterior side is continued over the margin of the epiglottis, and becomes suddenly thin only after it is fairly on the posterior side. In the new-born child the whole posterior side of the epiglottis is covered with a ciliated epithelium of 0.08–0.1 millim. in thickness.

In or about the second fourth of the posterior surface of the epiglottis—that is, in the vicinity of where the epithelium undergoes a transition to ciliated cells—bud-like or, at times, pyramidal structures may be seen among the epithelium cells; with their extremities they reach nearly to the horny layer and send through it to the surface a minute canal, whose course is sometimes straight, sometimes in spiral coils. These elements consist of elongated but more or less broad epithelium cells, whose somewhat broad bases usually rest upon the surface of the mucous membrane, while their pointed extremities are turned toward the free surface. These bud-like structures surround a canal, which, at the summit of the buds, immediately beneath the horny layer, becomes very much thinned and then terminates in the aforementioned minute canal. Whether or not these elements were the outlet ducts of acinous glands, I was unable to decide from the sections.

By the influence of certain reagents the epithelium cells of the laryngeal mucous membrane become converted into beaker cells, in the same manner as do the cells of other mucous membranes.

The submucous tissue of the anterior side of the epiglottis is more abundant and more loosely attached than that of the posterior side, and it may also as a rule be distinguished by the double course of its fibres.

Bundles also will be found which surround the cartilage of the larynx in a circular direction chiefly; and between these are other fibres that run lengthwise toward the base of the epiglottis, and gradually exceed the former in number.

From the point where the epiglottis becomes merged in the tongue, a portion of the longitudinal fibres are distributed to the latter.

The middle bundles of these fibres are purely elastic, and lift up the mucous membrane into the Plica glossoepiglottica; on the sides they again become intermingled with connective-tissue fibres which are somewhat loosely woven and frequently spread apart for the reception of fat cells. This group of longitudinal fibres can easily be followed down to the perichondrium of the epiglottis, from which at the same height the ligamentum hyoepiglotticum originates; while deeper down it is connected with the lig. thyreoepiglotticum. A few muscular fibres will also be found concealed in the deeper tissue; they belong to the M. thyreo-ary-epiglotticus, and run from the thyroid cartilage toward the lateral edges of the epiglottis or into the aryteno-epiglottidean fold.

On the lower part of the posterior side of the epiglottis the submucous tissue becomes looser and more abundant, so that the loosely adherent mucous membrane rises up like a knob at a point corresponding to the lower end of the cartilage. Fat cells and acinous glands are found here in great numbers. They are aggregated into groups of about 1 millim. in diameter, whose outlet ducts run pretty nearly at right angles to the free surface of the mucous membrane. Whereas at the upper free end of the epiglottis acinous glands are either entirely wanting or at least of rare occurence, lower down they are to be found arranged in small groups on either side of the median line of the cartilage and embedded not infrequently in the excavations of its substance. On approaching the prominence of the epiglottis the glandular aggregations become more numerous and are larger; at the same time their outlet ducts pursue a straight course, even after piercing the epithelium, whereas higher up they run in a straight direction only to the epithelium, where they bend at a right angle, and then, after running for a longer or shorter distance, again enter the epithelial layer. At this point they seemed to me—although I was unable to prove a direct connection between the two—to pass continuously into the bud-like elements already described above.

In the acinous glands of the larynx, as elsewhere, there can be demonstrated a structureless membrane lined with epithelium, whose cells have the form of a truncated cone and lie with their broad bases against the membrane. Their outlet ducts are lined with a layer of cylindrical cells, which at the prominence of the epiglottis and on the lower side of the false vocal chords sometimes carry cilia. The peculiarity of these outlet ducts is their great breadth, which in some cases may measure even 0.3 millim. It is not a rare circumstance to succeed here in isolating the structureless membrane of the outlet duct, thus enabling one at the same time to see the large stellate connective tissue corpuscles which lie upon and surround it with their processes.

On the posterior surface of the Dog's epiglottis the outlet tubes of the acinous glands are sometimes lined with a double layer of cuboid cells.

In the aryteno-epiglottidean folds the fibres of the submucous tissue follow the direction of the fold itself, and at the same time surround the bundles of the musculus thyreo-ary-epiglotticus. These muscular fibres, after bending around the cart. corniculata of the same side, radiate through these folds and then, hugging their outer side, they partly end there and partly continue on as far as to the lateral margin of the epiglottis, where they become inserted into its perichondrium. These striped muscular fibres

measure from 0.03–0.05 millim. in diameter and terminate in the following manner: the sarcolemma becomes diminished to a mere thread which, either with or without nucleated swellings, becomes lost in the surrounding connective tissue or among the fibres of the perichondrium.

Near the cartilaginous nodules of Wrisberg the fibres of submucous connective tissue pursue an irregular course; they cross and intermingle with the fibres that radiate from the perichondrium of the cartilages of Wrisberg and thus form numerous spaces for the reception of acinous glands, which here seem to be so numerous as even to lift up the mucous membrane.

In the Sheep, Pig, Cat, and other animals, lymph follicles lie embedded in the fold of mucous membrane at the entrance of the larynx.

In its further course the mucous membrane becomes folded so as to form the prominent upper (false) vocal chord, which with its rounded margin hangs down somewhat loosely; the mucous membrane then continues on downwards to line the Ventriculus Morgagni. When it folds itself into the so-called upper vocal chord, the mucous membrane, whose tissue is full of lymph corpuscles, carries with it into the fold a portion of the subjacent strongly elastic layer (fibrous membrane), whose fibres run in a purely longitudinal direction, so that the latter also becomes to a certain extent duplicated. The elastic fibres which are interwoven with this layer in considerable numbers also pursue a horizontal course; they start from the angle of the thyroid cartilage, and diverge as they pass backwards, a portion of them terminating in a sagittal direction, another portion bending round so as to enclose the posterior angle of Morgagni's ventricle. A ligamentum thyreo-arytænoideum superius cannot be demonstrated as a separate ligament. The fibres in these parts do not seem either to follow one particular direction or to unite in the form of a band; and a section made at right angles to the upper vocal chord shows only irregular elastic trabeculæ mingled with connective tissue. These trabeculæ, by diverging from one another at one moment and at the next uniting again, give rise to large spaces in which heaps of fat cells and agglomerations of glands of a considerable size lie embedded. A few bundles, however, pursue their course upwards as well as downwards, and become directly continuous with the longitudinal fibrous layer of the larynx.

In the Dog the elastic tissue of the upper vocal chord is not infrequently found to have become cartilaginous, the process having commenced in the arytenoid cartilage and spread anteriorly from it. Here, also, the horizontal direction of the fibres is much more plainly marked, and that bundle of fibres, which in Man bends downwards at the posterior angle of the ventricle of Morgagni, stands off here by itself in a prominent position and is covered by a mucous membrane; it gives to the upper vocal chord the appearance as if it were inserted into the recess of the ventricle of Morgagni. If the above-mentioned enchondrification has already taken place, the largest part of the glands will be found lying back of the cartilage, through which they pour their contents into the ventricle.

In Man a few smaller bundles of the musculus thyreo-arytænoideus externus are sometimes prolonged into the upper vocal chord and appear then as an independent muscle (M. Santorini).

At the borders of the aryteno-epiglottidean folds, throughout their entire length, the epithelium consists of layers of pavement cells which are also continued on as far as to the lower vocal chord over the surfaces of the confronting arytenoid cartilages. In animals the mucous membrane sends papilliform processes into the epithelium, while in Man they are limited to those protuberances of the mucous membrane which are caused by the cart.

corniculatæ; they measure sometimes 0.35 millim. in height and 0.1 millim. in breadth. On the other hand the upper vocal chords, and in Man also the walls of the Ventriculus Morgagni, are covered over with the same ciliated epithelium that was seen at the base of the epiglottis. In the ventricle the glands are composed of much smaller aggregations, all of which disembogue with a special, straight outlet tube, in exactly the same manner as this occurs in the confronting surfaces of the arytenoid cartilages.

While in the Ventriculus Morgagni the mucous membrane is separated from the cartilage by only a scanty elastic tissue, in the true vocal chord, and especially at its margin, this scanty layer becomes strongly reinforced by a prismatic compact band (lig. thyreo-arytæn. inf.) whose principal bundles—arising from the angle of the thyroid cartilage beneath its incisure —run toward the arytenoid cartilage.

The fibres of this band seem to be condensed into a single cord only in its anterior portion; posteriorly, however, they subdivide at an acute angle into several bundles, which seek various points of insertion. One of them, at the posterior angle of the ventricle, takes an upward course and so proceeds toward a portion of the lig. thyreo-arytænoideum sup., with which it becomes interwoven. The second and strongest bundle breaks up into two portions, one of which inserts itself into the fibro-cartilage of the processus vocalis, while the other inserts itself higher up into the spina inf. of the arytenoid cartilage, and so covers the processus vocalis. Finally, a third bundle—in position the deepest—breaks up in the neighborhood of the vocal process into five or six smaller bands, which at short intervals become inserted into the median surface of the arytenoid cartilage, into the inner side of the capsule of the crico-arytenoid joint, and even into the upper margin of the lamina cricoidea. They are separated from each other by vertical bands of connective tissue which start from the neighborhood of the cart. corniculatæ.

All these elastic bundles become united anteriorly, as has been mentioned already, into a more compact and hence smaller cord, which is prolonged for quite a distance into the very substance of the thyroid cartilage. The ligamentum thyreo-arytænoideum inferius, however, immediately after its egress from the thyroid cartilage, becomes thickened into a round swelling, which in fine sections is found to be composed of a dense intermingling of elastic fibres. In the new-born child this thickening is still more easily recognizable; here, however, the chief mass of it consists not so much of elastic fibres as of round and spindle-shaped cells, which are constantly increasing in length. A formation of cartilage I have never seen in this spot.

In the Dog the ascending bundle of the lig. thyreo-arytænoideum inferius, like the descending bundle in Man, is especially prominent, so as even sometimes to lift up the mucous membrane. It must be mentioned furthermore that the dividing line, between the vocal chord proper and the musculus thyreo-arytænoideus int., is much more sharply drawn in Man than in animals.

The prominent margin of the true vocal chord in Man is covered by a pavement epithelium, about 0.1 millim. in thickness, which, not only toward the ventricle of Morgagni but also toward the trachea, passes pretty suddenly into the ordinary ciliated epithelium; whereas posteriorly it is continuous with the pavement epithelium covering the aryteno-epiglottidean folds. The pavement epithelium of the vocal chords is broken up, moreover, by very large papillæ, which measure over 0.03 millim. in breadth at the base, and penetrate into the substance of the epithelium a distance of 0.05–0.06 millim.

Beneath the glottis the epithelial layer gradually grows thinner down to the trachea, and the same is true of the mucous membrane. The submu-

cous tissue, however, grows thicker along the anterior surface of the larynx, by offshoots from the membrana cricothyreoidea, and in its downward course it gains space for itself exactly in proportion as the prismatic belly of the musculus thyreo-arytænoideus int. recedes from the mucous membrane. Furthermore, the submucous tissue includes within its substance numerous glands which are flattened laterally in a marked degree, owing to the fact that they spread out more over the surface than into the deeper tissues. These glands congregate in greater numbers in the neighborhood of the cricoid cartilage; this is particularly the case in the posterior portion of the larynx, where at the same time the submucous tissue undergoes a corresponding enlargement.

The vessels of the larynx present no special peculiarities. The larger branches keep close to the cartilaginous framework, or at least run through the deeper portions of the soft parts. The smaller branches run up toward the mucous membrane, and there break up into a fine network.

The nerves offer equally as few characteristic features; their abundance is the only remarkable thing about them. Larger and smaller trunks can be followed as far as into the mucous membrane; their actual mode of termination, however, is not yet clearly understood. It appears that the muscular branches of the Laryngeus sup. and of the Recurrens, just before their distribution among the muscles, are provided with numerous ganglion cells. According to Luschka, the actual termination of the nerves takes place through the medium of pear-shaped or oval bodies, 0.0035 millim. in breadth, into each of which a delicate axis-cylinder enters, and usually terminates in the same with a swollen extremity.

B. Trachea.

The framework of the trachea is composed of 15–20 incomplete cartilaginous rings, which are open posteriorly and resemble somewhat a horseshoe in shape. Variations from this form occur, especially at the upper and lower ends of the trachea, where the cartilaginous rings frequently give off branches, upwards and downwards, which at various points become continuous with the neighboring rings; under these circumstances the separation of the individual rings may become a somewhat difficult task.

Between the open ends of the cartilaginous rings there are found in rare cases a few cartilaginous kernels which are also hyaline in structure. These too are sometimes found in animals.

In the Dog, Cat, Sheep, etc., the cartilaginous rings of the trachea approach more nearly to a complete circle than in Man. In a condition of rest they are so near to each other as almost to touch, and, during contraction of the muscular membrane of the trachea, they overlap each other, thereby forcing the mucous membrane into the lumen of the trachea in the form of a longitudinal fold, 3–4 lines in breadth.

From the lower margin of the cricoid cartilage to the first cartilaginous ring of the trachea, as well as beyond, between every two rings of the trachea, run strong bands of elastic and connective tissue which bind together the different parts of the framework. From the lower border of each separate ring a number of such bands radiate into the submucous tissue.

The inside of the trachea is lined with a mucous membrane, 0.13–0.15 millim. thick, which is characterized by its great richness in networks of longitudinal elastic fibres. Sometimes a very thin layer on its innermost side appears to be hyaline throughout. This has led to the assumption of a special basilar membrane on which lies, finally, an epithelial covering of ciliated cells, whose height varies from 0.06–0.075 millim.

Like the mucous membrane, the subjacent submucous tissue likewise shows a predominance of longitudinal fibres, which consist of connective tissue and contain an increasing number of elastic fibres the farther outwards we go. In the posterior portion of the trachea, which is free from cartilage, there is to be found beneath the mucous membrane a transverse layer, 0.8–1.2 millim. thick, of organic muscular fibres which are stretched out between the anterior surfaces of the ends of the cartilages. They either terminate—through the medium of their thin, delicate tendons—in the perichondrium of the cartilaginous rings; or—which is more rarely the case—they become lost in the substance of the mucous membrane.

This layer of muscular tissue appears to be broken up by quite strong intervening bands of connective tissue into subdivisions, of which it usually takes several to correspond to a single cartilaginous ring: the vessels and nerves, which supply the mucous membrane from behind, follow the course of these connective-tissue septa. It is not a rare circumstance, moreover, to find still shorter longitudinal muscular bundles lying on the outer side of the muscular layer; they spring from and end in the septa of the transverse layer, and are inserted into it like clamps. Finally, on the outermost side comes a layer of connective tissue whose fibres run longitudinally (fibrous membrane).

Similar but at the same time much stronger bundles of muscular tissue are also found in the trachea of the Dog and Cat. When they contract, the cartilaginous rings overlap each other like tiles, so that in horizontal sections two consecutive cartilaginous rings will be found in the same section. The section will present the appearance of two concentric cartilaginous bands, separated from each other by elastic tissue.

In the same animals, and also in the Rabbit, Sheep, and others, the transverse layer presents this peculiarity: it extends far beyond the ends of the cartilaginous rings and is inserted on their outer surface. It spans nearly a third of the circumference of the entire ring, and can contract so powerfully as to cause the free ends of the rings to greatly overlap each other, and even to become bent at their extremities.

The trachea is richly provided with acinous glands, which form a continuous layer over its anterior and lateral portions, and do not seem to lose their continuity even where the cartilaginous rings are most convex. On the posterior surface, where there is no cartilage, they are composed of several layers; some being between the mucous membrane and the muscular layer, others in the muscular layer itself, and others still lying behind it, so that the outlet tubes of the latter—which run in a straight direction toward the surface—must traverse the muscular layer.

The vessels form superficial networks in the mucous membrane of the trachea similar to those in the mucous membrane of the larynx.

The mode of termination of the nerves is not yet known. In the posterior fibrous membrane they present ganglionic swellings of considerable size and of a rounded oblong shape, whose greatest diameter is parallel to the long axis of the fibre. Their transverse diameter measures as much as 0.2 millim., while their longitudinal diameter measures two or three times as much.

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CHAPTER XX.

THE LUNGS.

By FRANZ EILHARD SCHULZE.

I. The Lungs of Mammals.

From the independent air tube which enters into each lung—bronchus—there is developed a system of smooth and solid-walled tubes—bronchi—which traverse the entire substance of the lung, like the branches of a tree. The single trunk first breaks up by acute-angled, dichotomous subdivision into a number of diverging branches, which, with each new subdivision, grow smaller. When they have diminished in size to a certain calibre—in Man about 4 millim. in diameter—they cease almost entirely to subdivide dichotomously and pursue a straight course, with constantly diminishing calibre, as far as to the neighborhood of the surface of the lung; at the same time, however, they give off laterally, at an angle of 45°, in spiral succession, smaller branches which likewise pursue a straight course. The side branches of these latter are given off in a similar manner, and again break up themselves into terminal branches by nearly rectangular dichotomous subdivision. For this reason, and partly also because one of the branches of this subdivision usually runs on in nearly the same direction as its parent branch, and because, futhermore, the subdivisions follow each other in planes which usually stand at right angles to each other, the course of these smallest bronchi is rendered a peculiarly zigzag one. Finally these smallest bronchi terminate with a diameter of from 0.3 to 0.2 millim. (the diameter of the bronchi is never less than 0.1 millim. even in the smallest Mammals—the Mouse, the Bat, etc.) in the *respiratory cavities.* These cavities also consist of round passages, which, at a distance of 2–4 millim. from the end of each bronchus, break up by acute-angled dichotomous subdivision into 2–4 small terminal branches which in their turn have short, similarly shaped lateral twigs. Both the terminal branches and their lateral twigs are usually funnel-shaped—called *infundibula*, on account of their comparatively narrow entrance and broad ending—and terminate blind.* These passages, however, do not like the bronchi possess uniformly thick, solid, tubular walls, but are lined with numerous contiguous *alveoli*, which consist of small polyhedral cavities, with rounded edges and angles, and open toward the lumen of the passage. These alveoli line not only the walls of the passages but also the lateral and terminal endings—the infundibula, and they are so closely packed together that the free, narrow borders of the alveolar septa constitute only a very small portion of the lateral boundaries of these passages, which

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* Net-like, open communication was incorrectly supposed to exist between neighboring air passages first by Bourgery (*Gazette des hôpitaux*, Juillet, 1842), and then later by Adriani (*de subtil. structura pulmonum*, 1847), Williams (in Todd's *Cyclopædia of anat. and physiol.*, vol. 5), and others.

are bounded almost exclusively by the walls of the alveoli themselves. For this reason I shall call them alveolar passages.*

Fig. 146.

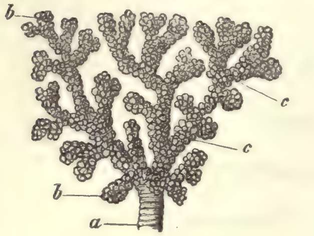

Fig. 147.

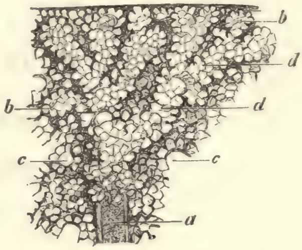

Fig. 146. A system of alveolar passages with infundibula from the border of an Ape's lung (Cercopithecus); filled with quicksilver. Magnified $\frac{10}{1}$. *a*, terminal bronchial twig; *bb*, infundibula. *cc*, alveolar passages.

Fig. 147. Section of a Cat's lung, filled with alcohol and hardened in the same fluid. Magnified $\frac{12}{1}$. *a*, terminal bronchial twig; *bb*, infundibula; *cc*, transverse sections of alveolar passages; *dd*, longitudinal sections of alveolar passages.

The lumen of these passages, so far as it is defined by the free borders of the alveolar septa, measures, in the adult Human being, 0.4–0.2 millim.; in medium-sized Mammals—the Hog, Dog, and Cat—0.2–0.15 millim.; in the Rat, about 0.1 millim.; in the Mouse and Bat (Plecotus auritus), 0.1–0.06 millim. The main trunks are always somewhat broader than the branches into which they subdivide. The breadth, moreover, increases with age, at least in Man.

The alveoli themselves—from 4 to 8 of which are found arranged in a radiating position about the transverse section of a passage or infundibulum—are usually hemispherical in shape in the new-born Mammal; later they become more polyhedral, through mutual pressure. They are shallowest, though at the same time separated by pretty broad septa, at the commencement of each system of alveolar passages (described above as the direct continuation of the finest bronchial twigs): they are deepest and only separated by narrow septa in the terminal processes—the infundibula, and especially at their fundus. In the alveoli of medium depth the dimensions of breadth and depth are about the same. The breadth of the alveoli, which, however, in certain regions of the system of alveolar passages varies but little, constantly increases with the age of the individual; whereas their depth decreases in advanced age. In Man the diameter of the alveoli averages, for the middle years of life, 0.15 millim.; immediately after birth it is 0.10–0.8 millim.; and in old age (according to measurements in a woman, æt. 60) the breadth is 0.25–

* *Intralobular bronchial ramifications* (Addison); *lobular passages* (Todd); *intercellular passages* (Rainey). While in the more familiar of the German text-books the infundibula are described as being directly attached to the last ramifications of the bronchi, descriptions of the structure of the parenchyma of the lung, similar to the one I have given here from my own investigations, may be found in Lerebouillet (*Anatomie comparée de l'appareil respiratoire*, 1838); Addison (*Philosophical transactions*, 1842; Rossignol (*Recherches sur la structure intime du poumon*, 1846); Le Fort (*Recherches sur l'anatomie du poumon, chez l'homme*, 1859); also (apart from the mention made there of open, net-like communication between the passages) in the articles "Organs of respiration" written by Williams in Todd's *Cyclopædia of anatomy and physiology*, vol. 5, 1859; and in a few other English authors.

0.4, the depth 0.1–0.2 millim. The dimensions of the alveoli of the larger domestic Mammals are about the same as in Man; in the smaller animals, however, they are very much less. I found the average breadth of the alveoli in the Rabbit to be 0.05, in the Rat 0.04, in the Mouse and Bat 0.03–0.02 millim. The 4–6 sided (though well-rounded at the angles) mouths of the alveoli appear everywhere to be somewhat narrower than the diameter of the alveoli themselves. This is due in the first place to the radiating arrangement of the air cells; in the next, however, to a thickening, slight though it be, of the free borders of the alveolar septa.

In describing the relations of the different textures it will be found advantageous to separate the bronchi, whose office is simply to *conduct* the air, from the parenchyma of the lung, which consists essentially of alveoli, and whose function is to assist directly in the exchange of gases between the blood and the air.

As regards their histological structure, the *bronchi* of Mammals are strikingly alike; that is, the tubes of the same calibre show as a rule either the same or a very similar texture, although differing in absolute size.

In the larger bronchi—those which measure 1 millim. in diameter and upwards and which we shall first describe by themselves—there can be made out as a rule, exclusive of the adventitia, four layers which are each characterized by a peculiar histological formation. The adventitia is made up of a variable quantity of loose fibrous connective tissue, containing here and there clusters of fat, and serving to connect the bronchus with the neighboring parts (vessels, lymphatic glands, nerves, alveolar tissue). The *external fibrous layer*, which is the outermost of the four layers and constitutes more than one-half of the entire thickness of the bronchial wall, consists chiefly of dense fibrous connective tissue in which cartilaginous plates are embedded. The cartilages of the bronchi, which contribute principally to their firmness and elasticity, retain in the first bronchial branches the same form which they possessed in the free bronchi, viz., that of flattened semicircular rings; in these first bronchial branches, however, they do not constitute a half cylinder, closed posteriorly by a membrane, but, branching on all sides, they form a perfectly tubular framework.

These half rings at first almost touch each other with their sharp edges; in fact, in some animals, the Hog for example, they somewhat override each other; but soon they become changed into irregular angular plates, provided with short processes. In Man this change takes place very soon, whereas in the larger animals (Horse, Cow) it occurs only after several bronchial subdivisions. These plates, which are not arranged in any special order, gradually grow smaller and more widely separated from each other, until finally nothing remains but a few delicate disks or spangles, occurring only at wide intervals, and then by preference at the angles of subdivision; in the bronchial twigs, whose diameter is less than 1.5–1 millim., they disappear altogether. Hence in very small Mammals (domestic Mouse and some varieties of Bats, e. g. Vesperugo Pipistrellus), whose largest bronchi scarcely attain this diameter, the cartilages may be altogether wanting in the lungs.

The cartilage cells, which are so numerous in the hyaline basis substance of the bronchial cartilages, are arranged in a peculiar manner. Throughout the entire cortical layer of a cartilage plate the cells are shaped somewhat like a flattened cake, and lie with their broad surfaces parallel with the external surface; while in the centre the cells are more round in shape (often likewise collected into oblong groups by the so-called secondary cartilage capsules) and are arranged in rows perpendicular to the surface. Hence, when especially examined, the two (inner and outer) superficial layers of the

firm basis substance of the cartilage, which are parallel to each other, seem to be connected by transverse buttresses.

The fibrous basis tissue, which at the same time serves as a periosteum to any plates of cartilage that may lie embedded in it, consists of longitudinal bands of parallel fibres of dense connective tissue, between which run smaller circular layers of the same tissue: in some places (especially in the outer portions of the entire layer) these may even alternate with each other like regular consecutive layers. It is traversed by longitudinal networks of delicate elastic fibres, which are closer and stronger in those places where they run from the sharp edge of one cartilage to that of the next, uniting the two in the direction of the long axis of the bronchial twig. While throughout the external portion of this fibrous layer adipose tissue may be seen in scattering clusters, the mucous glands are confined to the inner portion of the same layer, where they will be found to diminish in size and number with the calibre of the tube. In the larger bronchi these glands are situated not only in the purely fibrous interstices between the cartilages, but also on the inner side of the cartilaginous plates. In the former position, not being hindered in their expansion, they attain a large size and often protrude a considerable distance into the external portion of the entire layer; but in the latter, being limited on all sides in their growth, they usually assume a flattened, cake-shaped form. In the smaller bronchial twigs they are found only between the cartilages. With the multiplying ramifications of the bronchi they diminish in size and grow more and more scarce, until finally, with the disappearance of the cartilages, the glandular elements cease altogether. A straight outlet duct, lined with cylindrical epithelium, starts from each of these glands, and, piercing the inner layers of the bronchial wall, finally terminates on the free internal surface of the bronchial tube with a trumpet-like mouth. At some point in its course, and especially in individuals of an advanced age, the outlet tube undergoes an ampulliform enlargement.

Fig. 148.

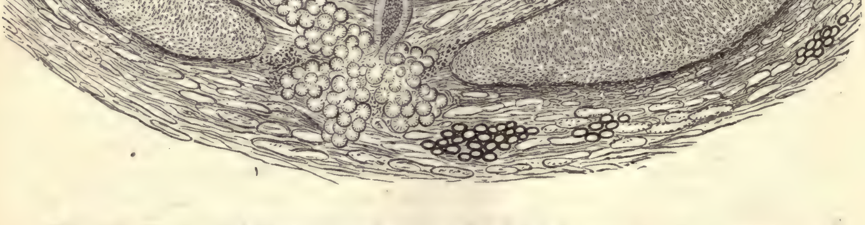

Fig. 148. Portion of a transverse section of a Man's bronchial twig, measuring 6 millim. in diameter. Magnified $\frac{30}{1}$. *a*, outer fibrous layer; *b*, muscular layer; *c*, inner fibrous layer with the hyaline boundary layer; *d*, epithelial layer.

Next to the outer fibrous layer, follows a layer of muscular tissue, consisting of dense circular bands of smooth muscular fibres. Inasmuch as the transverse section of each of these circular bands is itself circular in shape, it would

hardly seem correct to describe the muscular layer as a tube with smooth, even walls; nevertheless the muscular bands lie so close to one another and are so extensively united by net-like connections that, taken as a whole, it virtually represents a continuous layer. Its thickness depends in general on the breadth of the bronchial twig. In the largest bronchi, in the spots where there is no cartilage, it measures in the Horse about 0.5 millim.; in Man 0.3 millim.; in the Dog 0.2–0.1 millim.; in the Rat 0.005 millim.; in Human bronchi—4 millim. in diameter—0.1 millim.; and, in those measuring 2 millim. in diameter, only 0.05 millim. Beneath the cartilages the muscular bands are usually thinner.

In contrast with the two layers described above, which in transverse sections of the bronchi represent zones of pretty uniform thickness, the layer next in order, the inner fibrous layer, shows in the same view a regular alternation of broad and very thin portions, whose inner outline follows a wavy course. This is due to the presence of 14–20 longitudinal ridges which project into the lumen of the bronchus, and whose height depends chiefly on the degree of development of the entire layer,—which in turn is proportionate to the calibre of the tube,—but also in part on the degree of distention, at the time, of the bronchi; these being, as is well known, somewhat variable in their breadth. The most important and characteristic elements of this layer are strong elastic longitudinal fibres, which, while they do not form a uniformly thick circular layer, are yet apt to be found massed together in bundles in the longitudinal folds. The stroma is formed of a loose connective tissue, with delicate also chiefly longitudinal fibres; and on the inner side it is condensed into a hyaline boundary layer. On this layer—the so-called basis membrane—stands the *ciliated cylindrical epithelium*, which lines all the bronchi of such breadth as we have already mentioned.

Fig. 149.

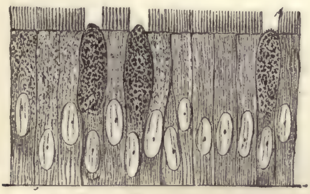

Fig. 149. Epithelium (fresh) of a Dog's bronchial twig, 4 millim. in diameter. Magnified 320 diameters.

In the larger bronchi the ciliated cylindrical cells measure about 0.08 millim. in length, while in the smaller bronchi they are somewhat shorter; their cilia are of medium length and move in the direction of the outlet. At pretty regular intervals between these cells stand a goodly number of the *beaker cells*,* which have only recently been minutely described by me. The Theca of these cells is entirely filled with a mucous-like material, throughout which are scattered numerous strongly refractile granules; when the parts are carefully examined, in a perfectly fresh condition, small balls of this substance may be seen pushing their way up through the upper rounded opening of the cell and at times even escaping from it. Moreover, between the lower ends of the cylindrical cells, which here are frequently either constricted or distended, cellular elements are found which are of an

* Max Schultze's *Archiv für mikroskopische Anatomie*, Bd. III., p. 192 and fol.

irregularly rounded shape, or else possess no characteristic form. As they possess no visible membrane, they must in all probability be young elements, whose destiny seems to be to fill the space previously occupied by others.

The principal difference between the larger bronchi, which we have already had under consideration, and those measuring 1 millim. and less in breadth —which we are now about to describe—lies in the structure of the external fibrous layer. Not to speak of the entire absence of cartilage and mucous glands, this external layer becomes so extraordinarily thin in the smallest bronchi that its thickness, in Human bronchi whose diameter is 0.4 millim., amounts to only 0.02 millim., and toward the final termination of the bronchus the layer disappears almost entirely. The outer fibrous layer is composed here of longitudinal bands of connective-tissue fibres, interspersed with delicate longitudinal elastic fibres. Next in order comes the muscular layer, which consists of smooth muscular fibres that pursue a circular course; toward the end of the terminal branch the layer gradually grows thinner and finally breaks up into individual ring bands, which are separated from each other by more or less broad fissures. These bands often consist of only a single layer of muscular cells, but are at the same time interwoven with delicate elastic fibres which traverse them at right angles.

The bands of strong elastic longitudinal fibres, which are so characteristic of the inner fibrous layer of the larger bronchi, are continued on into the smaller bronchial branches, where—mingled with the delicate fibres of a clear connective-tissue basis substance—they run in bundles along the inner side of the tunica muscularis, in the longitudinal folds.

Fig. 150.

Fig. 150. Portion of a transverse section of a Pig's bronchial twig, 0.4 millim. in diameter. Magnified $\frac{240}{1}$. *a*, outer fibrous layer; *b*, muscular layer; *c*, inner fibrous layer; *d*, epithelial layer; *f*, one of the neighboring alveoli.

At first the internal covering of epithelium still consists of the same ciliated cylindrical epithelia cells and intervening beaker cells which we have already met with in the larger bronchi. Toward the end, however, of the finest bronchial branches the epithelia cells gradually grow shorter until soon the dimensions of height and thickness become equal; finally the cells even assume a flattened form. In the region where the bronchi undergo the transition to alveolar passages, the cilia and the beaker cells disappear.

The bronchi receive their nourishment through capillary plexuses whose meshes are of an irregular shape in the outer fibrous layer, circular in the muscular layer, and somewhat elongated in the inner fibrous layer. The chief supply of blood comes from those branches of the Arteria bronchialis which lie in the Adventitia and outer fibrous layer; only the terminal bronchial branches are at the same time supplied in a few places by branches of the Arteria pulmonalis, whose capillaries then anastomose with those which originate in the bronchial artery. The blood, which in the capillary plexus has become venous, is then given up to the veins: the Vena bronchialis, which corresponds to the Arteria bronchialis, receives on its way to the hilus of the lung only that portion of the blood which comes from the walls of the larger bronchi; while from the smaller bronchi the blood goes directly into the Venæ pulmonales. Lymph vessels are found coming in large numbers, especially from the inner layers of the bronchi; they pursue their course along the outer connective-tissue envelopes of the bronchi toward the root of the lungs, where they enter the lymphatic glands, which are there situated.

Small ganglia, such as were first discovered by Remak, are found embedded here and there along the course of the nerves; these originate in the plexis pulmonalis and follow the course of the bronchi, ramifying over them and giving off branches which are evidently destined to furnish the chief nervous supply to the abundant smooth muscular tissue of these parts.

The alveolar tissue, like the bronchi, shows essentially the same histological relations in the lungs of different Mammals.

The parietes of contiguous alveoli, which belong to the same infundibulum or alveolar passage, fuse together as a rule into thin membranes (alveolar septa); where, however, the contiguous alveoli belong to neighboring infundibula or alveolar passages, this fusion does not always occur. In the latter case the separation is occasionally due to the presence of thin layers of a loose fibrous interstitial connective tissue; while between the different systems of alveolar passages this connective tissue is found with great regularity. In the lungs of all Mammals the alveolar parenchyma is subdivided by stiil thicker septa of connective tissue into polyhedral masses, called lobules. These diminish in circumference with the size of the animal. In Man they have a diameter of from 0.5 to 1 centimetre, and their irregularly polygonal (usually 4–6 angled) outlines may be seen shining through the pleura, or, in sections, they may even easily be recognized through the substance of the lungs. The interstitial connective tissue of the parenchyma of the lungs is firmly attached on the one side to the pleura, while on the other it passes continuously into the loose adventitious fibrous tissue which surrounds like a sheath the bronchi, the vessels and the nerves, and serves to bind them together.

The groundwork of the alveolar wall proper is a transparent, almost structureless layer of connective tissue, which is only here and there—especially in the thicker portions—distinctly fibrous, and in which may be found a very few scattered elongated oval connective-tissue nuclei, without any appreciable granular halo. This transparent basis substance is traversed by numerous elastic fibres whose peculiar arrangement imparts to the tissue of the lung its very characteristic appearance under the microscope. The elastic tissue occurs most abundantly in the principal channels of each system of alveolar passages. Here are found ring bands, composed of strong elastic fibres, which follow the course and enter chiefly into the composition of the free thickened borders of the strong septa that separate the lateral groups of alveoli: these ring bands, however, are not always closed so as to

form complete circles. Again we find the elastic tissue strongly developed in the septa at the bifurcation of the main alveolar passages: finally, it is also present at the always somewhat narrowed entrances of the lateral and terminal infundibula. From these denser bands of strong elastic fibres others of less width are given off which serve, on the one hand, as supports for the margins where several alveoli meet; and, on the other hand, as frames for the rounded polygonal entrances of all individual alveoli—whether they terminate directly in the passages or unite to form infundibula. Finally, from these smaller bands isolated elastic fibres of finer calibre are distributed in an arching direction over the alveoli, where they frequently form Y-like subdivisions, which anastomose with each other like the cords of a net.

Fig. 151.

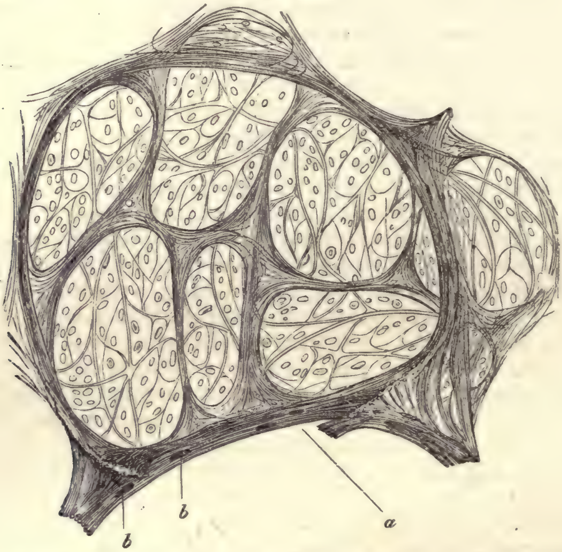

Fig. 151. Section through a lateral infundibulum. From the lung of an adult Human being, after it had been filled with and hardened in alcohol containing acetic acid. *a*, entrance from the alveolar passage into the infundibulum; the upper margin of the opening has been partially removed by the section. Magnified $\frac{20}{1}$. *b*, nuclei of smooth muscular fibres.

Delicate bands of smooth muscular tissue—which consist often of only a few isolated fibres, and are embedded in a connective tissue composed of delicate fibres—may be recognized scattered here and there between the more superficial layers of elastic fibres, in the borders of those septa which project most prominently into the lumen of the alveolar passages; this is especially the case at the beginning of the principal alveolar passages, where the free margins of the septa may still be looked upon as a direct continuation of the walls of the bronchi. The membranous walls of the alveoli are completely without muscular tissue, and even in the thicker borders of the individual alveolar septa I was not able to discover any smooth muscular fibres.*

* Although the majority of writers on anatomy miss, like myself, the presence of smooth muscular fibres in the walls of the alveoli, nevertheless they have been suppos-

The *respiratory capillary network*, which plays such an important part in the function of the lungs, is connected with the walls of the alveoli in a peculiar manner. It derives its origin from two sets of branches of the Arteria pulmonalis: first, from those which accompany the bronchi, and are situated in their adventitia and external fibrous layer; and second, from those which run through the interstitial connective tissue of the lobules and alveolar passages. When the blood has become arterial, it is carried by these capillaries into the collecting branches of the Venæ pulmonales, which usually lie on the opposite side of an entire group of alveoli, and the greater number of which accompany the branches of the Arteria pulmonalis in the reverse direction, although a few may traverse the tissue of the lungs by an isolated course. In the walls of the alveoli the capillary network encloses meshes either of an oval or rounded shape, or else angular with rounded angles. Where the alveolar wall is in addition surrounded externally by a dense layer of fibrous connective tissue—as is the case on the boundary surfaces of the several lobules, especially beneath the pleura—the capillary network spreads itself out in plane or slightly arched surfaces on the inner side

Fig. 152.

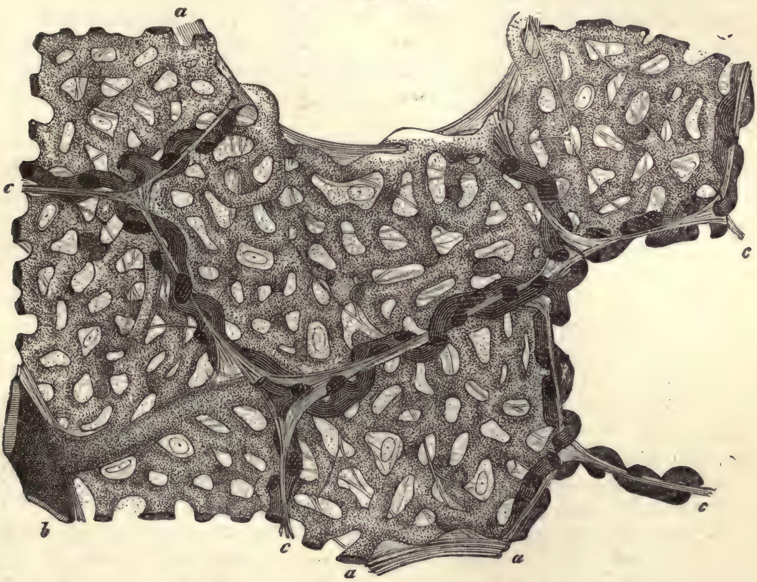

Fig. 152. Section through the alveolar parenchyma of a Human lung, injected through the Arteria pulmonalis. *a a*, free alveolar margins; *b*, small arterial branch; *c c*, alveolar walls seen in transverse section.

of the connective tissue wall; at the same time the capillary tubes lie embedded only to a very slight depth—at the very most, half way—in the basis membrane, whereas the greater part of their surface projects into the lumen of the alveolus. Where, however, as in the majority of cases, the walls

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ed to exist there, and have been described by Gerlach, *Gewebelehre*, S. 248; Moleschott in his *Untersuchungen*, Bd. vi., S. 390; Colberg, *de penitiore pulmonum structura*, Halis, 1863; Hirschmann, Virchow's *Archiv*, Bd. xxxvi., 1866; and by Piso-Borme, Moleschott's *Untersuchungen*, Bd. x., 1867.

of two neighboring alveoli become consolidated into a single thin membrane, the arrangement of the capillaries is different: instead of being situated each on the inner side of its own alveolar wall, the two capillary networks are now brought into immediate contact, and become united into a single though complicated network, whose transverse anastomoses traverse the common wall in extraordinary numbers. The meshes of these networks are very narrow (in Man about 0.001 millim. broad; in smaller animals only a trifle narrower) and do not lie in the same plane, but, frequently traversing the septum, they project first into one, then into the other of two contiguous alveoli.

If, in transverse sections of such alveolar septa, we follow the course of the capillaries, we shall see them projecting like loops, first on one side, then on the other of the septum. When the vessels are well injected, and the alveoli are but slightly distended, these loops are curved the most, and project into the lumen of the alveolus; whereas if the alveoli are more distended, the loops will not stand out so prominently from the walls; still even then they protrude the largest part of their side surfaces into the cavity. Should one wish to persuade himself that these free capillary surfaces possess—at least in many places—no independent connective-tissue covering, he will find the proof of it most easily in the capillary loops which run along the free borders of the alveolar septa. The diameter of the capillary tubes diminishes but slightly with the size of the animal, and measures in the lungs of the adult Human being—when the vessels are moderately full—from 0.006 to 0.008 millim.

Each separate alveolus does not possess its own special arterial and venous trunks; the capillary network originating in a single terminal arterial twig is usually distributed over several neighboring alveoli before it pours its contents into a small vein on the opposite side. In the region where the terminal bronchial twig passes into its appropriate system of alveolar passages, in the smaller bronchial branches, and close beneath the pleura, the capillaries originating in the Arteria pulmonalis anastomose richly with those which come from the bronchial arteries.

According to Wywodzoff's* investigations on the lungs of Dogs and Horses, the lymph vessels of the alveoli commence as small (anastomosing) spaces, which do not possess an epithelial lining, and which are situated in the connective tissue wall of the alveolus and always in the plane of that wall; their main branches follow first the direction of the elastic fibres and then the course of the capillaries, though not so exclusively, however, but that they frequently cross the latter and form large lacunæ in the meshes of the capillary vascular network. These first commencements empty their contents into two sets of lymph vessels: the one,† deeply situated, follows the bronchi and vessels directly to the root of the lung; the other, composed of comparatively superficial lymph vessels, surrounds like a network the end surfaces of the lobules, immediately beneath the pleura, and then, in Man, either follows an independent course to the hilus, or pours its contents at different points into the deep vessels.

The internal surface of the alveoli, as well as of all the infundibula and alveolar passages, is lined with a continuous epithelium which is uniform only in the fœtus, while in the adult Mammal it is irregular. Whereas in the alveoli of older fœtuses a uniform layer may still be seen, consisting of 4–6 angled, flat, closely packed epithelial cells, each of which possesses a

* *Wiener medizinisch. Jahrbücher*, Bd. xii., p. 1.

† Which also are fed from the bronchi, and have already been mentioned above.

membrane, granular contents, and a rounded transparent nucleus, in all individuals that have breathed for a short time already a few epithelial cells will be found, which have grown considerably larger and more transparent by the disappearance of their granular contents and the fading of the previously sharply outlined nucleus.

Fig. 153.

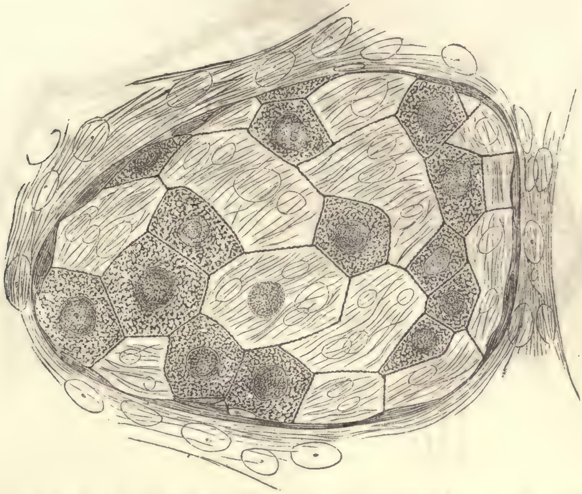

Fig. 153. Fundus of an alveolus; from a peripheral section that was made in a direction parallel with the pleura. The lung, which was taken from a child that had been born in the eighth month and lived two days, was previously filled with a solution of nitrate of silver.

In the alveoli of older animals * the polygonal or irregularly round epithelial cells, with granular contents and clear round nuclei, are seen either single or in small groups of from two to four (rarely more) among large, clear, thin, structureless plates, whose outlines are either irregularly angular or slightly wavy. These plates, moreover, are simply a modification of the earliest formed epithelial cells, in which the change described above, in speaking of very young animals, has undergone a still further development. This change, in all probability, is due to pressure of the expanding capillaries and partly to the tension of the distended alveoli (perhaps also in part, as Elenz intimates, to a sort of melting into one of contiguous epithelial cells).†

* In my researches I made use of the Cat, Dog, Rabbit, and Calf. The silver treatment proved ineffectual in the adult Human lungs which I was able to obtain, on account of the thickness of the pleura and the already too far advanced decomposition.

† The results of my investigations upon the alveolar epithelium of the lungs of Mammals, as stated here briefly, agree in all material points with the statements of Elenz (*Würzburger naturw. Zeitsch.* Bd. v.), of Eberth (*ibid.*), of C. Schmidt (*de l'épithelium pulmonaire*, *Diss.* 1866) and of Colberg (*Deutsches Archiv für klinische Medicin*, ii.). Other authors, like Addison, Remak, Rossignol, Reinhardt, Schröder Van Der Kolk, Adriani, Radclyffe, Hall, Schultz, Gerlach, Williams, Waters, Deichler, Zenker, Bakody, and Henle, deny altogether the existence of an epithelium in the alveoli; others, J. Arnold and Hertz, for instance, believe in the existence of an interrupted epithelium, whose nucleated cells occur only in the capillary meshes, leaving the capillaries, however, free; while others still, like E. Wagner, O. Weber, L. Meier, Chrzonszczewsky, Hirshmann, Baier, and Piso-Borme, describe an epithelium composed of perfectly uniform, closely packed, angular, nucleated cells.

The free margins of the basis framework which project into the lumen of the passages, the free borders of the alveolar septa, of the denser walls of separation between neighboring groups of alveoli, and of the narrow

Fig. 154.

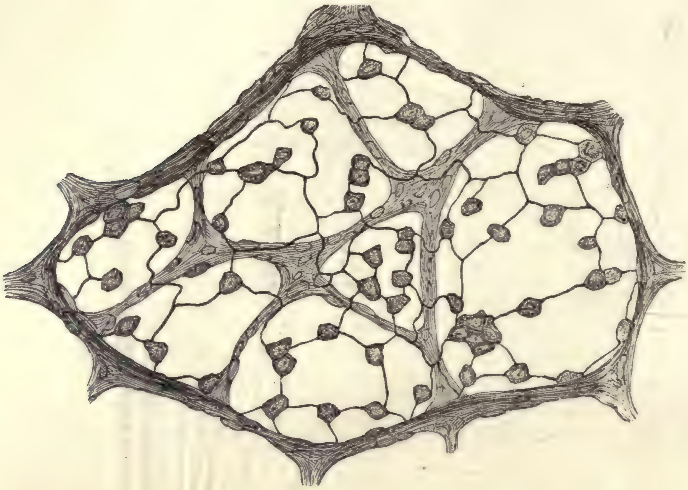

Fig. 154. Fundus of a peripheral infundibulum, situated close beneath the pleura; from an adult Cat's lung, which had been filled with a solution of nitrate of silver. Magnified $\frac{200}{1}$.

Fig. 155.

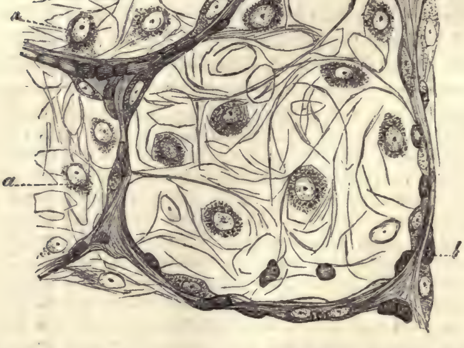

Fig. 155. Alveoli from a Cat's lung, which had been filled with and hardened in Müller's solution. *aa*, epithelial cells with granular contents; *bb*, capillaries containing blood corpuscles. Magnified $\frac{300}{1}$.

entrances to the infundibula, also those margins which occur at the points of bifurcation of main passages are lined only with these thin, transparent plates whose boundary outlines—marked out by the silver treatment—usually traverse them transversely. The granular epithelial cells never lie directly upon the capillaries, but always upon the wall of the alveolus, in the meshes of the capillary network; at the same time each mesh is not limited to a single epithelial cell, for then the number of the former would not suffice to hold them all. Very frequently in adult Human beings, more rarely, however, in other Mammals, the cells contain those small, round, black pigment granules which are also found in the alveolar walls of Human beings who are not very young. These granules are found in greater abundance in the interstitial connective tissue which separates the lobules of alveolar parenchyma, and also in the adventitious connective tissue which accompanies the bronchi and vessels; but they are especially abundant in the bronchial lymph glands. They are usually grouped in round or stellate heaps around transparent nuclei; more rarely will they be found scattered about diffusely, giving to the lungs of older Human beings the peculiar, black, speckled appearance with which we are familiar.

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II.—THE LUNGS OF BIRDS.

The *principal air passage*, which is a direct continuation of the free bronchus, traverses each lung from before backwards and finally terminates by a broad mouth in the abdominal air sac; on its way it gives off

laterally bronchial tubes, with pinnated side branches, which pursue their course along the surface of the lung, immediately beneath its accessory investing membrane (with which they are at the same time united throughout half their extent), and then also in part terminate in air sacs. From the membranous portion of the walls of these bronchi—that namely which is situated next to the surface of the lungs—only simple, smooth, low septa project inwards: these are connected together in such a manner as to enclose alveolar, honey-combed spaces like the meshes of a net; whereas from the sides of the bronchi which lie next to the parenchyma of the lungs, and also from some portions of the principal air passage, the so-called lung-pipes or air canaliculi (canaliculi aëriferi) are given off at a right angle. These lung-pipes are elongated tubes, which, when cut across, present externally a hexagonal outline, and whose voluminous walls contain the true respiratory tissue and compose the chief mass of the entire Bird's lung. They run side by side in a parallel direction, and their course, which at first is straight, becomes afterwards wavy or somewhat bent; at the same time they anastomose frequently, by open passages from one to the other tube. Their lumen, which in a transverse section appears circular, is bounded by the free inner borders of strong, membranous, annular partitions, which frequently communicate with each other

Fig. 156.

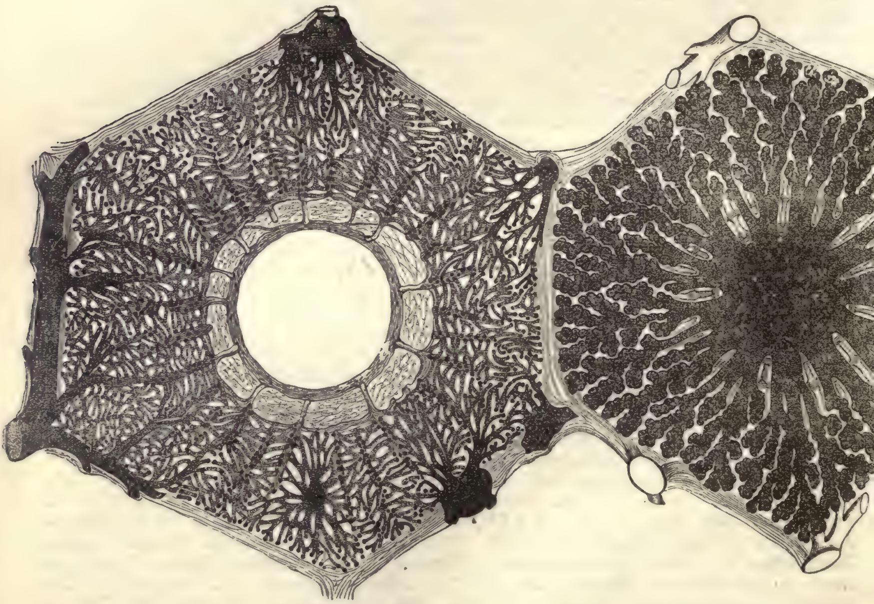

Fig. 156. Transverse section of two lung-pipes from the Goose. In the one to the right the air spaces are filled with a dark injecting material. In the one to the left the vessels have been filled by an injection into the Arteria pulmonalis.

by means of oblique anastomoses; these oblique partitions follow each other at pretty regular intervals and are connected together by numerous thinner intervening septa running in a longitudinal direction. Thus a sort

of network is formed which encloses honey-combed spaces whose groundwork constitutes the parenchyma of the voluminous walls of the pipes. From each such side niche of the honey-combed wall a few passage-ways enter into the parenchyma in a direction at right angles to and radiating from the long axis of the pipes; these passages, which at first are single and straight, soon give off branches like a tree—the branching being usually dichotomous and acute-angled—and finally terminate in small (in the Swan from 0.015 to 0.009, in the Goose from 0.010 to 0.006, in the Dove from 0.009 to 0.006 millim. in diameter) lateral and terminal oblong blind sacs, which when fully injected with the injecting material appear to possess numerous hump-shaped diverticles.

In the membranous parts of the walls of all the bronchi that run along the surface of the lung, four different layers may be distinguished similar to those in the bronchial walls of Mammals: viz., an external fibrous layer, a muscular layer, which however is not altogether continuous, an inner fibrous layer, and an epithelial layer. The external fibrous layer consists of fibrous connective tissue whose fibres follow chiefly a longitudinal course and are intermingled with delicate elastic fibres. Only at the beginning of the principal air passage do we find a few thin cartilaginous plates which clasp the tube throughout two-thirds of its circumference. Small clusters of adipose tissue are found scattered here and there in varying quantity, according to the condition of the individual as regards nutrition. The transverse bands of smooth muscular tissue, which lie on the inside of the external fibrous layer, do not constitute an entirely continuous layer, inasmuch as fissure-like openings exist between the bands. Beneath the cartilages the muscular tissue is entirely absent. The septa, which project from the membranous portion of the wall into the lumen of the bronchi, contain, especially near their free margins, strong muscular bands which are connected here and there with those just mentioned by means of more delicate muscular fasciculi. The inner fibrous layer is composed of a pretty thin stratum of longitudinal fibres of connective tissue, intermingled with delicate networks of elastic tissue, whose fibres also run longitudinally. This layer, which in a few places is thrown into low longitudinal folds, is spread out continuously over all the septa which project inwards and which are united together like a net: in fact it contributes in a very large degree to their formation. This inner fibrous layer is covered with a ciliated cylindrical epithelium, throughout which are scattered numerous beaker cells. In the final bronchial terminations this epithelium gradually diminishes in height. The membranous walls of the bronchi are nourished by a capillary network, which possesses elongated meshes and is distributed chiefly throughout the inner fibrous layer.

In those portions of the bronchi, in Birds, which lie immediately next to the parenchyma of the lung, the pulmonary pipes—which stand at right angles to the bronchus—are given off in such numbers and in such close proximity to one another that the bronchial wall in these places loses its membranous character and assumes more the appearance of a lattice-work. The framework of which the latter is constituted consists of strong bands of smooth muscular tissue, with a groundwork of fibrous connective tissue containing elastic fibres. This same connective tissue is then continued on over the free surface and constitutes the inner fibrous layer, which here possesses numerous capillary plexuses and is covered with ciliated cylindrical epithelium. From this muscular lattice-work, which surrounds the entrances to the pulmonary pipes, more delicate bands of the same tissue are continued on over the pipes themselves; at the same time they do not

extend into the thickened free borders of the transverse membranous septa —designated above as annular partitions—which are usually composed only of fibrous connective tissue together with delicate elastic fibres; the same is true of the less prominent longitudinal septa which connect them together.

The framework of the thick spongy outer wall of the pipe is formed of a very delicately fibred, almost homogeneous connective tissue, which is interspersed with networks of still more delicate elastic fibres and supports the rich capillary network to which the function of exchanging the gases is allotted. This respiratory capillary system emanates from the terminal branches of the Arteria pulmonalis, which run along the outer surface of the pipes and then penetrate at various points with their small terminal twigs into the parenchyma of the latter: from here these capillaries pass into the similarly situated commencements of the Vena pulmonalis. These capillaries often project a certain distance into the lumen of the air passages and are always firmly connected with the connective-tissue basis substance, in which they are more or less completely embedded; * they are very small in diameter and usually surround the terminal air passages in a transverse direction, inosculating freely in their course so as to form a network with elongated, sometimes almost fissure-like meshes. I have not yet succeeded in demonstrating the epithelial lining, which is undoubtedly present here.

Between the pipes, there are found in some Birds (Goose, Duck) pretty thick, in others (Dove) scarcely recognizable layers of a clear fibrous interstitial connective-tissue.

The air sacs of Birds—which must be considered as very large local diverticula of the bronchial walls—consist of a fibrous connective-tissue membrane, which is traversed by delicate elastic fibres and broad-meshed capillary networks, and is lined on its inner surface with a single layer of pavement epithelium, whose cells carry cilia only near the entrance of the sac.

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III.—THE LUNGS OF REPTILES AND AMPHIBIA.

The lungs of Reptiles and Amphibia are so nearly alike in their histological relations that they may be treated of here together.

In the continuous series, in which these animals may be classified according to the structure of their lungs, the Tritons and a few Perennibranchiata (Proteus, Menobranchus) occupy the lowest grade; each one of their lungs

* Rainey (in the *Med. chirurg. Transactions*, 1849, p. 50) expresses the view that the capillaries traverse the air spaces entirely independent of any connective-tissue support.

consists only of a simple, saccular enlargement—with perfectly smooth internal walls—of the bronchus that leads to it. The other Amphibia also possess saccular lungs, each of which is attached to its bronchus like a raspberry to its stem; they differ, however, from those just mentioned in having on their inner side a network of ridge-like elevations of unequal height. The highest of these ridges constitute a separate system of polygonal, usually quadrangular compartments—the principal meshes—at the bottom of which are smaller subdivisions, enclosed by similar ridges of less height, which start from the principal ridges; each of these smaller subdivisions is in turn subdivided into still smaller compartments, and so on, until finally there is produced a number of rounded, polygonal—usually quadrangular or pentagonal—niches or alveoli, whose flattened bottoms lie immediately upon the wall of the lung-sac. The ridges which constitute the side walls of these alveoli stand upon the wall of the lung at a right angle, and the alveolar openings look toward the general air cavity of the lung-sac.

In the elongated tubular lung of Snakes and Amphisbæna the thick-walled, anterior portion is characterized by the depth and complicated structure of its mesh-like spaces. The surfaces of the principal ridges, which stand at right angles to the wall of the lung, are not smooth as in the Amphibia, but carry along their sides secondary networks of ridges; hence the alveoli which these enclose no longer rest with their bases upon the wall of the lung, but upon the wall of the ridge, and moreover their openings do not look toward the general cavity of the entire lung-sac, but directly into the mesh-like space that is enclosed by the principal ridges to which they belong. Toward the posterior end of the lung of Snakes and Amphisbæna the entire network of ridges again becomes simpler; they gradually diminish in height and often finally disappear altogether, leaving the final termination of the lung a mere blind membranous sac with smooth walls.

While the lungs of many Saurians (Anguis fragilis, Lacerta agilis, Scincus bistriatus) do not differ materially in the construction of their air spaces from the simple lung of the Amphibia, in others, as for instance the Chamæleontes, the general cavity of the lung-sac will be broken up into two or more large compartments; this separation, which is not perfectly complete, is accomplished by the projection of one or more large septa from the wall of the lung-sac toward the mouth of the bronchus—the septa themselves, like the rest of the pulmonary wall, being lined with small ridges enclosing alveoli.

In Turtles there are large numbers of these septa traversing the entire cavity of the lung and blending perfectly with the tubular prolongation of the bronchus into the pulmonary cavity; these, moreover, are so arranged as to divide each lung into a number of contiguous blind sacs—usually arranged in two rows—which no longer communicate with each other and can only be entered from the bronchial prolongation.

The alveolar parenchyma, which covers the inner wall of these several subdivisions, is constructed in a similar though more complicated manner than that of the Snake's lung. Here too the principal ridges do not possess simple smooth walls, but carry on their side surfaces other ridges which are united together in the form of a net; and these last carry other ridges, and so on.

In the Crocodile the alveolar parenchyma, though constructed on the same principles, is arranged in a more complicated manner and is more richly developed; the principal air spaces, which in the lungs just described were shaped like a sac, here become narrowed down to rounded passages, yet without forming actual, solid-walled bronchi, such as belong to Mammals.

In all Reptiles and Amphibia the histological basis of the entire lung tissue consists of a fibrous connective tissue, interwoven with delicate networks of elastic tissue, and containing stellate pigment cells which are filled with a black, granular material. In some animals (e.g. Salamandra maculata and many Frogs) these cells are very abundant; in others (Chamæleon, Scincus, Testudo græca, Emys europ., Coluber natrix) they are found only in small numbers; while in others still (Lacerta agilis, Alligator sclerops) they are wanting altogether. The continuation of the bronchus, which projects a greater or less distance into the lung, consists in Snakes of a semicylinder, in Turtles of a straight tube, perforated with round openings, and in Crocodiles of a somewhat branching tube; its walls, which consist mostly of fibrous connective tissue, contain numerous smooth cartilaginous (hyaline) rings, which anastomose with one another and whose sharp confronting edges are connected together by a tense mass of longitudinal elastic fibres.

Smooth muscular tissue is found embedded in the connective-tissue stroma of the parenchyma of the lung, and indeed in such abundance often as to constitute the chief bulk of the entire tissue. Already in the simple lung-sacs of the Tritons there may be found a thin layer of muscular fibres following a circular course; * but in all the lungs that possess alveoli strong muscular bands will be found to constitute the main supports of the retiform ridges which enclose alveolar meshes, and they are especially developed in their thickened inner free borders. These strong and compact main trunks branch out into thinner bundles; and even the latter give off a few isolated muscular fibres, which traverse the shallow bottom of the alveoli near their inner surface.

In the lungs of Reptiles and Amphibia the nerves consist of medullated and non-medullated fibres, in the course of which may be recognized here and there small collections of ganglion cells; these were first thoroughly investigated in the Frog's lung by Julius Arnold,† who described them as bell-shaped cells with granular contents, into which enters, on the concave side, a darkly outlined nerve fibre whose axis cylinder terminates in the nucleolus. From this latter, according to Arnold, delicate processes are given off which traverse the substance of the nucleus in a radial direction, and are connected with a system of delicate threads which traverse the granular cell-contents and finally terminate in another nerve fibre—the so-called spiral fibre—which winds around the straight entering fibre in spiral turns.

From the arterial twigs that bring the venous blood to the lungs there is developed a capillary network which is distributed uniformly throughout the walls of the alveoli, and whose irregularly round meshes do not exceed in breadth the diameter of a capillary vessel—which differs in various animals according to the size of the blood corpuscles. This respiratory capillary network traverses uninterruptedly the low alveolar septa, whereas on the summit of all the higher ridges, on the internal surface of the tubular continuation of the bronchus, and also in the posterior portion of the lungs of Snakes and Amphisbæna, it passes into a system of broad-meshed capillaries whose chief function is probably that of supplying nourishment.

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* In accordance with my own investigations I must corroborate the statement of H. Müller (*Würzburger naturw. Zeitschrift*, Bd. ii., p. 131), who, in opposition to Reichert and Leydig, maintains the existence of a thin layer of circular muscular fibres even in Triton tæniatus.

† Virchow's *Archiv*, Bd. xxviii., p. 431, 1863; *Centralblatt für die med. Wissensch.*, 1864, No. 42; Virchow's *Archiv*, Bd. xxxii., 1864.

All respiratory capillaries are attached to the wall of the alveolus by only one side: hence the greater part of their surface would project free into the cavity of the alveolus if they were not completely covered by a *continuous flattened epithelium.*

Fig. 157.

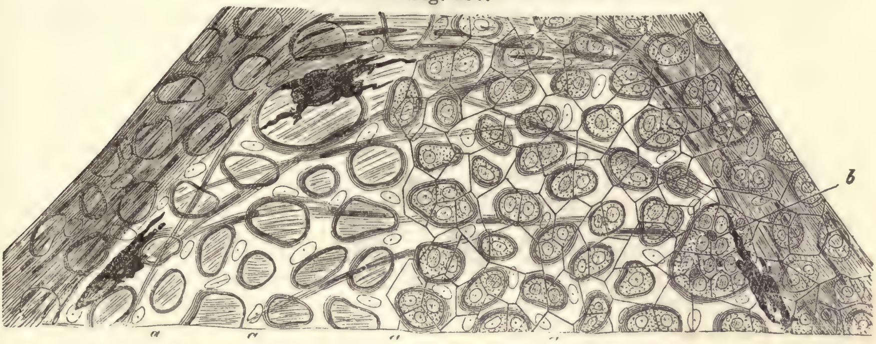

Fig. 157. Portion of an alveolus from the lung of Rana temporaria. The epithelium is not represented on the left side. Magnified $\frac{220}{1}$. *aa*, ends of capillaries; *b*, a conglomeration of narrow, cylindrical epithelial cells.

The edges of the large polygonal cells of which this alveolar epithelium is composed fit each other exactly; these cells, moreover, give off thin transparent plate-like processes which extend over that portion of the surface of the capillaries facing the air cavity, and send plug-like prolongations—containing usually the nucleus of the cell together with a certain amount of granular protoplasma surrounding it—into the capillary meshes; these processes extend deep down so as to rest upon the connective-tissue stroma of the alveolar wall, and thus completely fill the empty spaces of the capillary network.

Fig. 158.

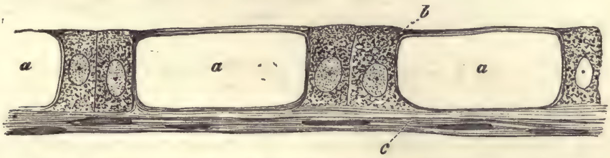

Fig. 158. Optical transverse section of an alveolar wall, from the lung of Rana esculenta. Hardened by osmic acid. Magnified $\frac{340}{1}$. *aa*, capillary spaces; *bb*, the nucleated plugs of the epithelial cells; *c*, muscular fibres of the alveolar wall.

These plug-shaped processes, which contain the nucleus and granular protoplasma of each cell, may usually be found at the angles of the individual epithelial cells, so that several plugs can lie together in the same capillary mesh. Still many cells are also found which carry their nucleated process more in the centre, and with it fill up completely a capillary mesh.*

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* Although the results of my investigations essentially agree with the statements of Elenz and C. Schmidt in regard to the pulmonary epithelium of Amphibia, yet I must differ from them as regards the alveolar epithelium of the Reptilian lung, for here also I found that all epithelial cells—even those that were entirely flat—were provided with nuclei, and I was unable to discover any structureless non-nucleated

While now the respiratory surfaces of the Reptilian and Amphibian lung are covered by such a flattened epithelium,* the free borders of all the higher septa and ridges, as well as the internal surface of the bronchial prolongation, are covered with a ciliated, cylindrical epithelium which is usually rather low and in which may be found in a few places a large number of beaker cells. The entire non-respiratory posterior portion of the lung of Snakes and Amphisbæna is lined with a simple though continuous layer of small, polygonal, slightly granular, flattened epithelial cells.

Fig. 159.

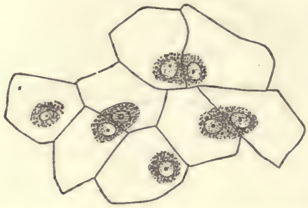

Fig. 159. Epithelium taken from the inner alveolar wall of a Testudo græca. Magnified $\frac{200}{1}$.

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IV.—THE LUNGS AND THE AIR BLADDER OF FISHES.

The lungs of Dipnoi unite anteriorly into one common cavity, but posteriorly they constitute separate sacs. On their internal surface they possess a system of ridges which are connected together like a net and enclose polygonal alveolar meshes; while anteriorly—as is the case in the Snake's lung—these ridges are so arranged as to form a complicated system of secondary alveoli, some of which may also be seated upon the side walls of the principal air cells, in the posterior portion they all run at right angles to

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plates. By filling up the lungs with Müller's fluid and likewise immersing them in the same fluid, not only is the epithelium lining the respiratory spaces of Amphibia and Reptiles rendered perfectly distinct in all its outlines, but it even becomes possible to separate the epithelium either partially or entirely from the subjacent parts and to dissect it into its individual cells.

* Here and there in the midst of the alveolar epithelium, round groups of cells (10 to 30) are met with—most frequently in the Frog's lung—which have a more cylindrical shape and entirely fill one of the larger capillary meshes. These cells, like the beaker cells, would seem to possess to a limited extent a secretory function (fig. 157 *b*).

the walls of the lung-sac and consequently form alveoli which only open directly into the general air cavity. The relations of the finer textures in the lungs of Lepidosiren do not differ materially from the description given of the lungs of Amphibia. Here also the groundwork seems to consist of a fibrous connective tissue, interspersed with large stellate pigment cells. In the inwardly projecting ridges dense bands of smooth muscular tissue may be found which are most fully developed in the neighborhood of the free margins, and whose bulk increases with the height of the septa. On the internal surface of the alveolar walls and lower boundary ridges there is spread out a respiratory capillary network whose round meshes scarcely exceed the diameter of a capillary in breadth. This network is covered with a single layer of large, flattened epithelial cells, which, as in the Amphibia and Reptiles, send short nucleated processes down into the capillary meshes.

The air bladder of Fishes, although purely a hydrostatic apparatus without respiratory network, is yet morphologically closely allied to the lungs. The microscopical relations of the textures of these bladders vary just as much as do the macroscopical. At one time the air bladder consists of a simple sac, at another it is partitioned off by indentations and deep constrictions ; again, the walls may be perfectly smooth, or the internal surface may be traversed by projecting septa and ridges. The principal tissue of which the bladder consists is a dense fibrous connective-tissue membrane, situated usually on the outermost side of the organ, immediately beneath the peritoneum. This layer consists of long, fine, in many Osseous fishes peculiarly stiff fibrils of connective tissue, which at one time all run parallel to each other in a transverse or oblique direction, while at another they run in bands that cross each other at right angles : in the latter case the layer frequently represents two perfectly separable layers—the fibres of the outermost layer running longitudinally, those of the one beneath it transversely.

Occasionally ossification takes place in this outer fibrous layer, as for example in Cobitis fossilis, Acanthopsis, Ophidium imberbe ; in Cobitis it assumes the form of a connected capsular grating, with round meshes.

In the loose fibrillated connective-tissue stroma of the layers which come next in order—and which here may be grouped together under the title of the internal layer—elastic lamellæ are often found lying parallel to the surface ; in most of the Osseous fishes these remain very delicate, while in some kinds, especially in the anterior vesicular portion of the air bladder of the Cyprinoids, they grow to be compact fenestrated membranes. Between these elastic lamellæ—e. g. in Esox lucius, Perca fluv., Gadus Callarias, Gadus Zota, etc.—peculiar, oblong, quadrangular, delicate, elastic, small plates are often found, which, with the exception of the oval nucleus that usually occupies the centre, are completely transparent and structureless, and when made free roll themselves up like a leaf. They are commonly found piled up, one on top of the other, in small packages, but may easily be separated. A very peculiar connective-tissue formation exists in the thick, satin-like layer of the Sturgeon's air bladder. This consists, with the exception of a loose, scanty, fibrillated connective-tissue stroma, entirely of spindle-shaped, comparatively short, in the centre thick, flattened though rounded fibres, which in some places will be found collected into closely packed larger bundles ; while in others they may easily be separated into smaller single, uniformly shaped fibres. Besides some small, short, dark, longitudinal markings, which may be interpreted as perhaps the commencement of connective-tissue corpuscles, no real structure can be made out in these strongly refractive, and—a point to which I would here call especial

attention—also strongly doubly-refractive * elements. When boiled and also when treated with acids they become very much swollen and dissolve rapidly into gelatine.

Muscular tissue—at one time of the transversely striated, at another of the smooth variety—is mingled in various ways with the connective-tissue groundwork of the air bladders. The air bladders of Polypterus bichir and Amia are surrounded externally, immediately beneath the peritoneum, by an envelope consisting of two superposed layers of transversely striated muscular fibres which cross each other at right angles. In Amia each layer consists of only a single thickness of fibres, lying side by side; while in Polypterus there are several thicknesses. In a third Ganoid—Lepidosteus osseus—bands of transversely striated muscular fibres lie, not on the external surface of the air bladder, but in the here richly developed internal membranous ridges and beams which surround the alveoli; these muscular bands are connected together in the form of a network either by direct communication, or through the medium of tendinous cords. In the Sturgeon, however, a continuous layer of smooth muscular tissue will be found in the external fibrous layer. A few Osseous fishes—e. g. Trigla, Dactyloptera, Zeus—possess sharply outlined plates or bands of transversely striated muscular tissue only in certain spots of the external surface of the air bladder; while others—the Cyprinoids—possess in the anterior portion of the air bladder, embedded in the internal layer, in the median line of the ventral side, a long band of smooth muscular fibres which run in a transverse direction; this band, moreover, in the neighborhood of the point of constriction, spreads itself out into a completely circular ring. In the posterior portion of the bladder two longitudinal bands may be found, of smooth muscular tissue, which are embedded in the outermost portion of the external layer, and whose fibres run transversely. Again, in other Fishes—e. g. Esox lucius, Gadus Callarias, Perca fluv.—a continuous thin stratum of smooth muscular fibres is found in the inner layer.† Finally, the muscular tissue may be entirely wanting, as in Cobitis and others.

In some Fishes—e. g. Accipenser and Salmo—the vessels which supply the air bladder always originate in the aortic system and consequently carry arterialized blood; they break up into a simple wide-meshed capillary network which is destined to supply the parts with nourishment and which finally empties its contents into the veins of the trunk. In many others, however, peculiar vascular formations are met with in the outer portion of the inner layer: these were first carefully studied by Johann Müller, and by him placed in the category of wonder-plexuses. Arterial vessels break up suddenly into at one time diffuse, at another more localized, radiating, fasciculated or tuft-shaped systems of tubes, from which are developed—either directly or after their union into a few larger vessels—arborescent capillary networks. From these capillary networks, which are spread out over the internal surface of the air bladder, proceed venous wonder-plexuses—either directly or after their union into a few larger veins—which are so interwoven with the arterial plexuses that a transverse section of the entire wonder-network shows a pretty uniform distribution of arterial and venous tubes side by side.

The continuous epithelial covering, which lines the inner surface of every

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* The optical axis corresponds to the long axis of the fibres, which, as in the muscular fibres, are *positively* doubly refractive.

† Leydig describes in Esox a layer of smooth muscular fibres in the outer layer, where I was unable to find them.

air bladder, consists in the Sturgeon, and also, according to Leydig, in Polypterus bichir, of ciliated cylindrical cells; in the Osseous fishes, however, it consists of a single layer of flattened epithelial cells which assume a somewhat different character over the capillary plexuses that originate in the arterial wonder-networks; that is to say, they are higher, more cuboid in shape, with opaque granular contents, and therefore more like gland cells in appearance. Moreover, their glandular function is rendered still more probable by the circumstance that, like glandular epithelium, they completely line the fissure-like or pocket-shaped depressions in the capillary body.

Principal works on the minute structure of the lungs and air bladder of Fishes.

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PETERS. Ueber die Lungen von Rhinocryptis, in MÜLLER'S Archiv. 1845.
FISCHER. Versuch über die Schwimmblase der Fische. 1795.
JACOBI. De vesica aërea piscium. 1840.
BERLAK. Symbolæ ad anatomiam vesicæ natatoriæ piscium. 1834.
VAN DER HOEVEN. Ueber die zellige Schwimmblase des Lipidosteus. MÜLLER'S Archiv. 1841.
J. MÜLLER. Vergleich. Anatomie des Gefasssystemes der Myxinoïden. 1841. Und Ueber die Eingeweide der Fische; in den Verhandl. der Berliner Akademie. 1845.
REINHARDT. Om svommeblaeren hos Familien Gymnotini. 1852.
LEYDIG. Anatom. histolog. Untersuchungen über Fische und Reptilien. 1853.
LEYDIG. Kleinere Mittheilungen zur thierischen Gewebelehre. MÜLLER'S Archiv. 1854.
LEYDIG. Lehrbuch der Histologie. 1857.

CHAPTER XXI.

THE KIDNEY.

By C. LUDWIG.

If we examine the fresh kidney of a Mammal, after it has been cut open from the papillæ to the fibrous capsule, the naked eye will readily distinguish on the cut surface the striped medullary portion from the granular cortex; both of which portions are arranged concentrically. If the blood and urinary vessels of the kidney have been injected with materials of a different color, we shall notice further subdivisions, radiating in character, and occupying not only the medullary but also the cortical portion.

Fig. 160.

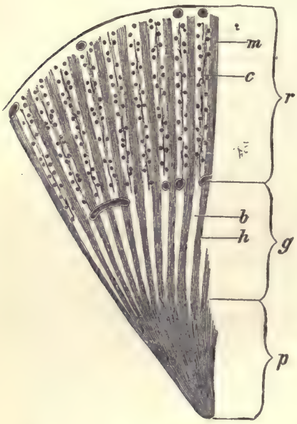


Fig. 160. Section of a Dog's kidney, made in a direction parallel to the uriniferous tubules and blood-vessels, both of which are injected. *p*, papillary portion; *g*, boundary portion of the medulla; *r*, cortex. The dark bands of the medulla (*h*) represent bundles of uriniferous canals, which are continued on into the cortex (*m*)—medullary radii. The clear spaces in the medulla (*b*) correspond to the positions occupied by the bundles of blood-vessels of the boundary portion. The clear spaces of the cortex (*c*), which are dotted with black points (glomeruli), designate the position of the labyrinth.

In the medullary portion bands of the same color as the material injected into the uriniferous canals radiate from the papilla as centre toward the cortex.

These bands are contiguous in the papilla and a little beyond it, so that up to that point the medullary portion appears uniformly colored. This part of the medulla is called the *papillary portion.* The farther these bands are removed from the papilla the wider apart they become separated, until on nearly reaching the cortex they run at distances from each other which about equal their own diameter. The spaces between these bands are filled by other parts whose color is the same as that with which the blood-vessels are injected. The part of the medulla, in which the bands of tubules and blood-vessels alternate, is called the *boundary portion* of the medulla. In the cortical portion there are also bands, which, from the direction in which they run and from the intensity of their color, are evidently the immediate continuation of the bands of uriniferous tubules in the medulla. These bands that come from the medulla and extend almost to the extreme border of the cortical portion are called by the name of *medullary radii* (pyramidal processes). The spaces which remain in the cortical portion after the removal of the aforementioned parts receive their color chiefly from the material injected into the blood-vessels; to this part we will give

the name of *labyrinth of the kidney* (cortical portion, in the narrower sense of the term).

By directing the microscope to these differently colored portions it will be seen at once that each of them consists of a large number of canals, that communicate either with the blood-vessels or with the uriniferous tubules. These two varieties of canals make up by far the greatest part of the substance of the kidney.

URINIFEROUS TUBULES.—1. Course and diameter. The uriniferous tubule, by changing frequently its course in its passage through the kidney, traverses a comparatively very long distance ; in one part of its course it remains isolated, but in another it joins with the neighboring tubes to form a common canal. At the same time it changes its diameter very greatly in the different localities through which it passes.

All the uriniferous tubules originate in the labyrinth. Each one begins as a spherical dilatation (capsule of the glomerulus). After passing through the narrow neck of the capsule it dilates into a broader tubule which follows a very winding course toward the medulla; on reaching the boundary portion this curved and hitherto broad portion of the tube becomes suddenly narrower, and runs as a delicate straight canal more or less deep into the medulla (descending or closed branch of the loop), where it makes a sharp turn (Henle's loop) and then returns in a straight direction toward and into the cortex (ascending or open branch of the loop). On its return to the cortical portion this fine canal does not seek the same spot from whence it came ; on the contrary, it avoids the labyrinth and hugs the margin of the nearest medullary radius. Sooner or later, however, it leaves this straight course and winds its way as the so-called *intercalated* portion among the convoluted canals of the labyrinth. From here it returns by a curved course (the convexity of the curve being toward the external surface of the kidney) to the medullary radius, where it ceases to run as an independent canal. Other canals coming from different directions join with it at this point to form the straight and broad collecting tube.

Before following this tube any farther on its way we must render an account of the several changes in diameter which the tubule has undergone, from its first commencement in the cortex to its final junction with the collecting tube in the medullary radius. It has already been mentioned that in every instance, after the tubule has ceased its winding convolutions, and is passing down toward Henle's loop, it undergoes a material decrease in its diameter. The distance through which it retains this small diameter is not in all cases the same. Often it retains the contracted diameter as far as into the descending branch of the loop, but just as often the narrow canal, already before reaching the loop, will expand into a broader one, whose diameter, however, is very much smaller than that of the convoluted portion. The tubule retains this new calibre nearly up to the point where it passes through the convolutions of the intercalated portion. When about to commence these convolutions the canal becomes a trifle narrower, but immediately afterwards commences to expand, and continues to do so almost to the very periphery of the region in which the intercalated portion lies. In some kidneys this dilated portion of the intercalated tubule presents this remarkable feature, that its hitherto cylindrical calibre now becomes irregularly distended at different points. This is caused by the dilatation of the wall of the canal into small pouches which vary in size and number. In the last coil made by the intercalated tubule, before joining the collecting tube, its calibre again becomes narrowed for a short distance.

In its course as an isolated tubule the diameter of the canal changes seven times, viz.: (1), narrowing from the capsule to the neck; (2), enlargement from the neck to the convoluted portion; (3), narrowing at the point where it proceeds toward the loop; (4), enlargement on its approach to the open branch of the loop; (5), narrowing at the commencement of the intercalated convolutions; (6), enlargement in the course of the convolutions; and finally, (7), narrowing on its passage from the intercalated portion to the collecting tube.

We must return now to the description of the collecting tube. This is formed, as we have already seen, by the union, at the cortical end of the medullary radius, of several hitherto isolated tubules in a similar manner to the union of the branches at the top of a tree. For a short distance from its commencement the collecting tube still receives a few tubules, but after that it runs as an isolated and straight tube as far as into the papillary portion, remaining all the time in the tract of a medullary radius. When the several collecting tubes have reached the papillary portion they commence to unite, and this continues to take place until in the place of originally a large number of tubes there remain only a few. This union of the tubes is always two-cleft. At first all the collecting tubes that lie side by side in a medullary radius unite together, and then the principal tubes of two neighboring medullary radii, and so on. The terminal canals resulting from this union of the tubules two by two—the so-called ductus papillares—finally open on the free surface of the papillæ. As to the diameter, the rule holds good that the canal is a little broader than either of the two canals which unite to form it.

2. The grouping of the tubules into primitive cones. A limited number of uriniferous tubules bear a more intimate relation to one another

Fig. 161.

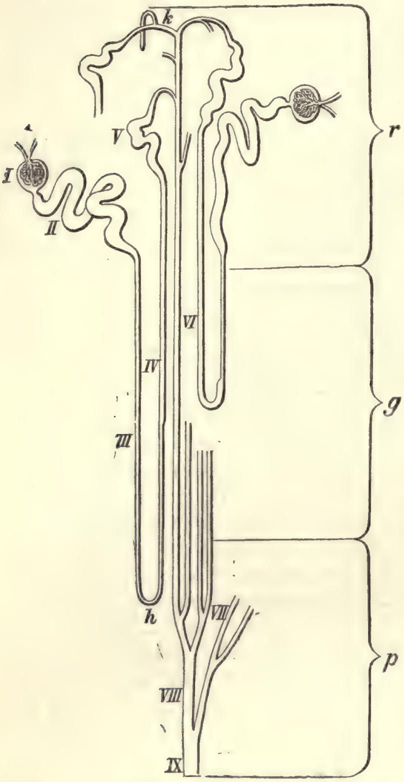


Fig. 161. Diagrammatic representation of the course of the uriniferous tubules; Human kidney. *p*, papillary portion; *g*, boundary portion of the medulla; *r*, cortex. I, Capsule of the glomerulus, which becomes constricted at its neck, and then passes into the convoluted portion of the canal, II. At the boundary between the medullary and cortical portions the convoluted canal becomes narrower, and then pursues a straight course as the descending branch III of Henle's loop: after passing through the loop (*h*) it retraces its course as the ascending branch IV. To this is attached the intercalated piece V, which approaches the summit *k* of the collecting tube VI by an outwardly arching course. The collecting tube then unites with others VII of the same medullary radius to form the principal tube VIII, which in turn unites with other principal tubes to form the papillary duct IX.

than to all the rest. This relationship is expressed by the fact that all their collecting tubes run side by side in the same medullary radius, and finally pour their contents into a single excretory duct. But even in their isolated course the tubules, which form by their union the collecting tubes of a medullary radius, are arranged in such a manner that they can be readily recognized as belonging together. All the parts belonging to such a subdivision present in their totality somewhat the appearance of a cone or bottle, whose apex or neck is located in the papilla, while its base is in the cortex. Inasmuch as the kidney, so far as its tubular composition is concerned, is to be looked upon as an aggregation of many such primitive cones, it will be necessary to learn their structure in order to understand the kidney. In describing it we shall commence at the papillary end of the tubules and proceed toward the cortex.

Each of the principal tubes, by whose union the papillary ducts are formed, approaches the centre of the transverse section of the medullary radius either just above the papilla or still within it. At this point the principal tube receives a number of accessory branches. So far as we know, this branching takes place within a limited region of the medulla, so that each collecting tube gains its independence a short distance above the papilla. All the collecting tubes that start from one main trunk run in close proximity and parallel to one another almost to the very periphery of the kidney; they constitute the chief part of the bundle of tubes which is designated by the name of medullary radius. On reaching the periphery the collecting tube breaks up into a number of uniform branches, each of which will then run as an isolated uriniferous tubule as far as to its very end.

Fig. 162.

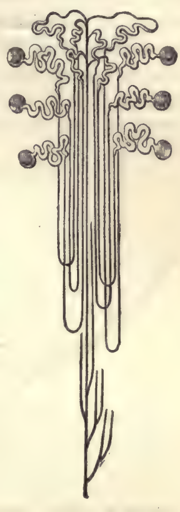


Fig. 162. Diagrammatic representation of the course pursued by the uriniferous tubules in the formation of a primitive cone.

Each of the uriniferous tubules, on leaving the collecting tube, makes a short arch and then, as the intercalated piece, winds its way along the base of the cone, as far as to the very periphery of the kidney, so that on penetrating from its fibrous capsule into the kidney, the first thing one meets is convoluted tubules, the greater part of which belong to the intercalated variety. From this region the intercalated tubules return again to the axis of the cone (medullary radius), where they assume a straight course, and pass down through the spaces that remain between the collecting tubes, in the medullary radius. After passing down a certain distance into the medullary portion they commence to form loops, and this change takes place in such a manner that throughout the entire boundary portion of the medulla, canal after canal forms itself into a loop. That branch of the loop which passes up toward the convoluted portion of the tubule, continues, after making the loop, to lie near its appropriate bundle of collecting tubes, but soon it gradually leaves it to continue its final course as convoluted tubule. In the cortex these convoluted tubules surround the medullary radii like a sheath, in so far as they are not already enveloped by the coils of the intercalated tubules.

3. The arrangement of primitive cones in pyramids or renculi.

If we bear in mind that the principal tubes of the primitive cones join together in the papilla to form papillary ducts, we can readily understand

how a pyramid is formed by the juxtaposition of numerous primitive cones, each one of which is connected with a single duct or papilla. In this connection there are only two points that require special consideration. The first relates to the origin of the slit-shaped spaces, which occur in the boundary portion of the medulla and are filled with blood-vessels. They are produced in the following manner. At the point where the cortex ceases, the medullary radius also loses abruptly the sheath of cortical substance which has up to that point surrounded it. The mantle of the primitive cone therefore undergoes a decided constriction at this point, similar to that which occurs in the passage from the body to the neck of a bottle. If we imagine two or more such flask-shaped bodies laid side by side in such a manner that their bellies and the tips of their necks touch, there must necessarily remain a space between every pair, just at the point where the bodies pass into the necks. The other point relates to the manner in which the collecting and urinary tubes join together to form papillary ducts, the peculiarity of which is necessitated by the rounded, blunt shape of the papilla. The way in which this takes place is well illustrated in the accompanying figure, which represents a longitudinal section through the papilla; by reference to this it will be seen how the tubes, coming from all sides and usually by crooked routes, unite to form the short and few papillary ducts.

Fig. 163.

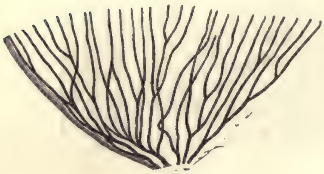


Fig. 163. Junction of the terminal urinary canals in the papilla. Diagrammatic.

4. Structure of the wall of the uriniferous tubule. The uriniferous tubule changes the structural character of its wall as frequently as it does its diameter or the direction of its route. The thin wall of the spherical capsule, so far as we are able to learn its structure, consists simply of a mosaic of cells, similar to that of which the blood- and lymph-capillaries are composed; its outer surface is woven over with connective-tissue. This connective-tissue is most strongly developed about those capsules which lie nearest to the medulla.

The coil of vessels enclosed within the capsule also possesses its own special enveloping membrane, which fits closely to the vessels. We shall speak of it farther on.

From the neck of the capsule down to the very beginning of the papillary duct, the wall of the canal consists of a basis membrane (tunica propria) and of an epithelium lining its inner surface. With the means of dissection at our command the basis membrane appears as a rule homogeneous; only now and then do we succeed in demonstrating by the aid of carmine imbibition the presence of a nucleus in the substance of the membrane. With a solution of silver we can sometimes bring to view in the convoluted tubules, though only for a short distance, the same design which characterizes silver-treated blood- and lymph-capillaries. The basis membrane is hyaline, elastic and very easily made to swell; it can be readily obtained alone.

The epithelium, lining the inner surface of the basis membrane, is nucleated and consists of a single layer. The shape of the nuclei is everywhere the same; they are spherical, sharply outlined, and possess in their interior numerous granules. The body of the cell, on the other hand, varies.

In the convoluted tubules the nuclei are embedded at tolerably regular distances from one another in a pulpy mass. In this mass there are numerous fissures, which can be seen in every transverse section, but are especially distinct when filled with the coloring matter that has been injected into the

uriniferous tubules. These fissures occur, however, at very irregular intervals; in a word, the breaking up of the mass into cell-bodies, each one surrounding its appropriate nucleus, seems here to be wanting. The epithelial pulp is

Fig. 164.

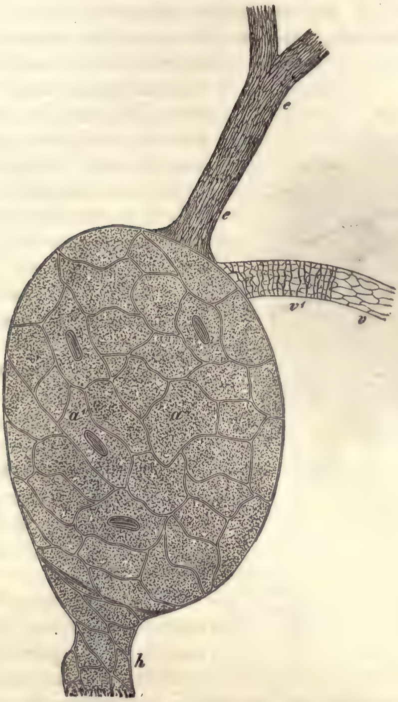


Fig. 164. Capsule of the glomerulus, from a Rabbit's kidney; silver-treated and tinged with carmine.—The endothelial cells of the capsular wall (a); in some cases, with oval nuclei (a'). The endothelium is continued on into the neck (h).—The vas afferens (v) shows at v' the silver markings which enclose the muscular rings; at v it only shows the outlines of its endothelium. In the vas efferens (e) the silver lines surround the spindle-shaped endothelial cells.

Fig. 165.

Fig. 165. Tunica propria of a convoluted uriniferous tubule; detached epithelial masses are contained within it.

Fig. 166.

Fig. 166. An isolated portion of a convoluted tubule, still filled with its epithelium. Moistened with very dilute hydrochloric acid.

only loosely attached to the basis membrane, and in a fresh condition it can easily be forced out of the isolated fragments of tubules. If this is accomplished by a shrinking of the tunica propria, then the masses of lining substance that have been driven out appear as long, cylindrical, firmly coherent pieces.

The extent to which the epithelial mass encroaches upon the calibre of the canal depends on the amount of stretching the tubule may have been subjected to. If the tubule has been put upon the stretch by the artificial production of a urinary stasis, the ring of epithelium lining the canal will be narrow; if the kidney, however, was empty before death, the same ring will appear broader. The pulpy lining must therefore be intimately connected with the basis membrane, following as it does all its changes in form. The material composing the pulpy cell-bodies is not homogeneous; besides numerous oil drops there will be found in the amorphous basis substance other dark granules, which can be cleared up by dilute acids. These deposits produce such a degree of opacity, that, as a rule, without previous acidulation it is impossible to recognize the nuclei; this characteristic has procured for the lining of the convoluted tubules the name of dusky epithelium.

Fig. 167.

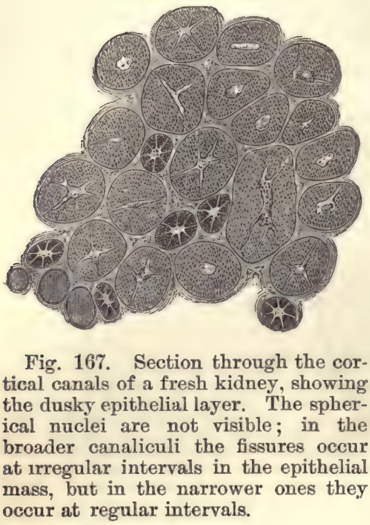


Fig. 167. Section through the cortical canals of a fresh kidney, showing the dusky epithelial layer. The spherical nuclei are not visible; in the broader canaliculi the fissures occur at irregular intervals in the epithelial mass, but in the narrower ones they occur at regular intervals.

In the narrow tubules that lead to and return from Henle's loop, there is found, in the place of the dark and solid epithelium just described, a transparent and thin epithelium, lining the wall of tubule in a continuous sheet, but bulging out into the calibre of the canal wherever there happens to be a nucleus.

At that point beyond the loop, where the diameter of the uriniferous tubule again becomes greater, the mass of substance surrounding the nuclei is broken up in a peculiar manner, so that midway between every two nuclei there is seen a fissure which extends down to the wall of the canal and forms with it an acute angle, open toward the cortex. This gives to the epithelium the appearance of being composed entirely of individual cylindrical cells, which have been made to overlap one another in the direction from the medulla to the cortex, like the tiles of a roof.

In the tubules of the intercalated portion the epithelial lining again assumes the pulpy appearance which characterized it in the convoluted portion. In the collecting tubes, as far as to the papillary

Fig. 168.

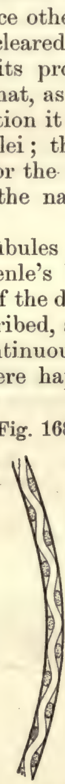


Fig. 168. An isolated portion of a narrow uriniferous tubule, with delicate, thin, transparent epithelium, and alternating swellings due to the presence of nuclei.

ducts, the epithelium consists of sharply defined cylindrical cells which lie with their broad bases resting on the basis membrane and their stumped apices turned toward the lumen of the canal. In the papillary ducts the canals lose their basis membrane, so that here the epithelium alone constitutes the wall of the canal; this is similar to what takes place in the sudoriferous glands where the epidermis forms the continuation of the canal.

Fig. 169.

Fig. 169. From an ascending branch of the loop; to show the arrangement of the epithelial cells, piled up on top of each other like the tiles of a roof.

Inasmuch as the uriniferous tubules of all Mammals can be referred to the above plan, as regards their structure, course, and arrangement, we should expect that the kidneys of the different varieties of Mammals would resemble each other in their smallest details, provided the dimensions in thickness and length of the tubules were also everywhere the same. The only difference would then be in the number of the tubules which go to form a kidney. These premises, however, do not accord with the facts; the striking differences which exist between the kidneys of different Mammals prove that, in respect to the dimensions of the primitive uriniferous tubules, a large margin is allowed this class of animals. The most superficial estimates, made from transverse or longitudinal sections through the kidney, teach that not only the absolute dimensions of length and thickness vary in different kidneys, but that also the relations which the lengths of the different portions of the canal bear to each other are variable. And besides, independently of everything else, this point is proven by the varying proportions

Fig. 170.

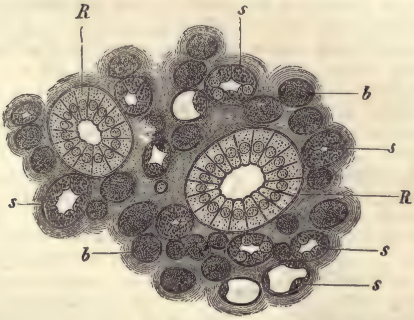


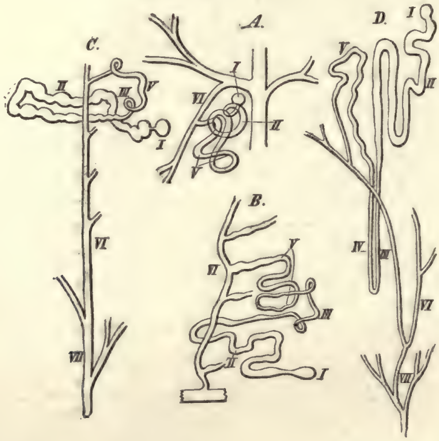
Fig. 170. Transverse section of the medullary portion (fresh), showing the epithelium of the uriniferous tubules in that locality. The dark circular objects are transverse sections of blood-vessels (*b*). The epithelium is perfectly clear, so that the circular outlines of the spherical nuclei may be seen through them. (*R*), Collecting tubes: the individual epithelial cylinders are distinctly separated from each other. (*s*), Narrow and broad branches of the loop. Between the canaliculi runs a layer of fibrillated connective tissue.

of cortical to medullary substance in different kidneys. It will be impossible to arrive at any more accurate results concerning these for the function

of the kidney undoubtedly so important measurements, until we shall be able to isolate the uriniferous tubules more readily and in a less brittle condition than is to-day practicable.

From the information that has been gathered concerning the anatomy of the uriniferous tubules in other classes of Vertebrates, the following points deserve to be mentioned here :—

Fig. 171.



The diagrammatic outline drawing (Fig. 171 D *) is taken from a Dove's kidney. It will be noticed at once how strong the resemblance is to the uriniferous tubule of Mammals. The several subdivisions which we make in the latter are also to be found here, and they occur in the same order. The same agreement is preserved in the epithelium of the two kidneys. As far as our present knowledge goes, the uriniferous tubules of all Birds are made on the same plan as those of the Dove.

Fig. 171 C represents the course followed by the uriniferous tubules in the kidney of the Testudo. The capsule and its neck I, the swollen and tortuous portion of the canal II, the narrowing into which it next passes III, the broadening which then succeeds it, and which occurs just before its union with the collecting tube—all these are likewise present here. This diagram differs from that of Mammals only in two respects : the outlines of the convoluted portion of the tubule are sinuated and not smooth ; and the narrow portion which lies between it and the intercalated portion is differently formed from the loop in the kidney of Mammals. In the neck of the capsule of the Turtle's kidney the epithelium is low; in the convoluted portion it is deep and sometimes pigmented; in the narrow portion it is clear and low.

Fig. 171 B represents the uriniferous tubule of the Frog. The elongated capsule passes into the convoluted tube II, through the elongated neck I. The convoluted tube becomes narrowed on arriving at portion III, and then gradually broadens out again into a second subdivision V, which possesses numerous convolutions and terminates in the collecting tube. The wall of the capsule is surrounded by a strong layer of connective tissue; its epithelium is low and clear, and often provided with cilia. In section II the epithelium consists of deep polygonal cells; in III it is low and clear; while in the analogon of the intercalated portion it is deep and opaque.

In the course which they pursue and in their construction, the uriniferous tubules of the Triton are very similar to those of the Frog.

Fig. 171 A. Diagram of the uriniferous tubules of Cobitis fossilis. The capsule is relatively small, the neck very long. From the neck to the collecting tube, the tubule follows a winding course; at the commencement and at the end it has a comparatively large diameter, but in the middle of its course, for a short distance, it is somewhat nar-

* The group of figures included under No. 171 were designed by Hüfner.

rower. The depth of the epithelium corresponds to the diameter of the canal; it is everywhere clear.

The simplest kidney known to us belongs to Bdellostoma Fosteri; its uriniferous tubules consist of a capsule whose neck passes into a broad tube which runs a short distance and then joins the collecting tube. Concerning the epithelium of this, the most primitive of kidneys, nothing is known.

Blood-Vessels.

As a rule the kidney is supplied with blood by the renal artery; under certain circumstances, however, it can be nourished, though perhaps only partially, by the lumbar and suprarenal arteries, whose delicate branches anastomose with those of the renal artery on the tendinous capsule of the kidney. Although the medullary and cortical portions and the tendinous capsule of the kidney are supplied from one main trunk, yet the capillary branches and arterioles are distributed in a special manner in each of these three parts.

Blood-Vessels of the Cortical Portion.—The renal artery sends by far the greatest part of its blood through the cortical portion; the main branches that supply it do not stop on the way to form plexuses, but pass straight on into the cortical portion, where they break up, very soon after their entrance, into numerous small arteries, the arteriolæ interlobulares.

In a section of the kidney, where the cut has been made in a direction parallel to the last-named arteries, they can be seen running between every two neighboring medullary radii; in other words, their course as a general rule lies where several primitive cones border on each other. By far the greater portion of these branches become invisible to the naked eye so soon as the medullary radii cease; a few of them, however, pierce through the outermost layer of the cortical portion and enter the tendinous capsule. Every art. interlobularis, on its way through the convoluted tubules, gives off branch after branch in rapid succession, that is, just as often as it passes near the dilated end of a convoluted tubule (capsula glomeruli). Hence all the art. interlobulares distribute to the cortical portion at least as many branches as there are commencements of uriniferous tubules there; it is likewise very probable that no other branches besides these are given off by them in the cortical space.

Each of these arterial terminal branches (vas afferens glomeruli) runs in a straight course from the point where it is given off to the nearest terminal dilatation of a uriniferous tubule. Some of these very numerous vasa afferentia, before reaching the spherical end of the uriniferous tubule, give off a very delicate branch which breaks up at once into capillaries that send their blood into the network of capillaries surrounding the uriniferous tubules. But all vasa afferentia, whether they have previously given off a branch or not, pass directly to the terminal dilatation of the uriniferous tubule and pierce its wall directly opposite the commencement of the convoluted tubule (the neck). Once within this space, the vas afferens breaks up into a bundle of capillaries (glomerulus) which unite again within the hollow of the capsule to form a small venous branch (vas efferens glomeruli). This small vein, which is of about the same size as the vas afferens, lies in close contact with the latter from its very start, and, as a rule, pierces the capsule at the same spot where the vas afferens enters it.

Concerning the arrangement of the vessels within the glomerulus, the following only is known. Immediately after its entrance into the spherical dilatation of the uriniferous tubule, the vas afferens breaks up into from 4

Fig. 17

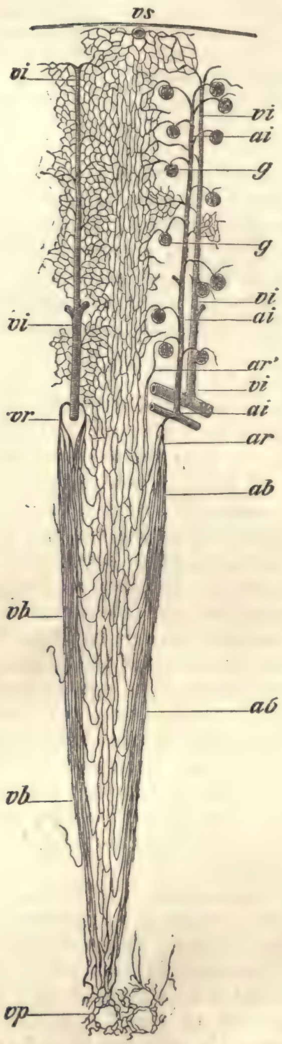


Fig. 172. Diagram of the circulation of the blood in the kidney.—*ai*, arteria interlobularis, which gives off numerous vasa afferentia to the glomeruli *g*; the vas efferens coming from the latter empties its blood either into the wide-meshed capillary network of the medullary radii, or into the narrow-meshed plexus of the convoluted canals. At the periphery of the cortex these plexuses unite to form the Venæ stellatæ *vs*; while in the labyrinth of the cortex they empty their blood into the Venæ interlobulares *vi*. Two sets of vessels penetrate into the medulla: the art. rectæ veræ *ar*, from the renal artery, and the vasa efferentia of those glomeruli which surround the medulla *ar'*. From the arterial bundle *ab* of art. rectæ originate the capillaries which supply the uriniferous canals of the medulla. These various networks then return their blood through the Venulæ rectæ, very many of which are grouped together in a bundle *vb*. The branches of this bundle unite into a single small venous trunk *vr*, which pours its contents into a larger renal vein.—The mouths of the urinary canals in the Papilla are surrounded by a venous network *vp*.

to 8 branches, which proceed toward the neck of the canal in the most arching manner and with the greatest divergence possible. On its way every branch gives off numerous twigs, and the latter, as it appears, gradually unite in the centre of the capsular space to form the vas efferens. The capillaries which originate from one of the main branches of the arterial vas afferens very frequently unite again to form a single vein, thereby giving rise to a venous system which corresponds exactly to the arterial distribution. When this occurs, the glomerulus breaks up into individual vascular lobules, which are attached together only by their arterial and venous ends. Although the glomerulus is at no point adherent to the membrane of the capsule, yet the wall of the capillaries is by no means in immediate contact with the fluid contents of the capsule; this is prevented by a layer of cells covering the outer wall of the vessels. These cells have spherical nuclei and ill-defined outlines.

The exact relations of this covering are still but little known; to all

Fig. 173.

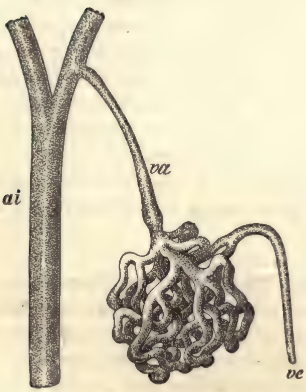


Fig. 173. Glomerulus from the Cat's kidney. Magnified $\frac{300}{1}$. *ai*, arteria interlobularis; *va*, vas afferens; *ve*, vas efferens.

Fig. 174.

Fig. 174. Distribution of the vas efferens in a lobulated glomerulus (from the Hog's kidney).

appearances it surrounds each of the lobules of which a glomerulus is usually composed, and hence serves to bind its individual vessels together. The coverings of two neighboring lobules are not united at their extreme peripheries; if they are united at any place, it can only be at the roots of the lobules.

To return to the vas efferens glomeruli. When it has left the capsule, it proceeds toward its appropriate medullary radius, or, if there happen to be none, as in the outermost portion of the cortex, toward the convoluted tubules; it then subdivides into a number of capillary vessels which form an anastomosing network. All the vasa efferentia, with the exception of those situated in the immediate neighborhood of the medulla, subdivide in a similar manner into capillary plexuses, and the peripheral vessels, of all the groups of capillaries which have originated in neighboring vasa efferentia, communicate with one another, so that in this way there is established a continuous capillary network throughout the entire cortex. This network, however, is not confined to the cortex alone, for it communicates also with

the capillaries of the medulla through the capillary network surrounding the medullary radii.

The meshes of the vascular net surrounding the convoluted tubes of the cortical portion are narrow and somewhat circular in shape; those of the network traversing the medullary radius are broader, and are drawn out in the direction of the course taken by the straight tubules. The capillaries forming this network are at no point adherent to the uriniferous tubules; between the walls of the blood-vessels and those of the uriniferous tubules there will be found everywhere slit-like spaces, which are frequently filled with fluid.

The capillaries just described unite at short intervals into veins, and the smallest of these unite rapidly into larger ones. In the outermost layer of the cortical portion, where there are no glomeruli, these veins come together in the form of a star (venæ stellatæ). From the centre of the star, the common trunk passes on into that part of the cortex which is provided with glomeruli and medullary radii, and chooses a position in close proximity to the arteria interlobularis. By the side of this the vein then pursues its course toward the boundary region, between the medulla and cortex, taking up on its way thither very numerous larger and smaller veins which have originated in the capillary network of the cortex. Within the cortical region the veins are always embedded in such a manner that the lumen continues to remain open, even when the vessel is empty.

Fig. 175.

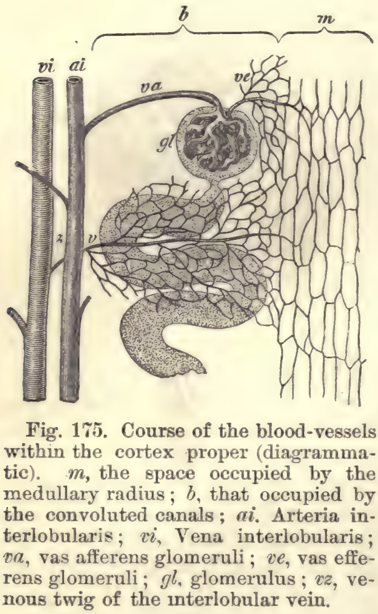


Fig. 175. Course of the blood-vessels within the cortex proper (diagrammatic). *m*, the space occupied by the medullary radius; *b*, that occupied by the convoluted canals; *ai*. Arteria interlobularis; *vi*, Vena interlobularis; *va*, vas afferens glomeruli; *ve*, vas efferens glomeruli; *gl*, glomerulus; *vz*, venous twig of the interlobular vein.

Blood-Vessels of the Medulla.—The blood which supplies the medulla flows with but few exceptions through straight trunks—the arteriolæ rectæ; they all approach the medulla from the direction of the cortex (figure 172 *ar* and *ar'*). The name of artery, in the complete sense of the word, is merited only by a portion of these, while the others merit it simply because they pour their blood into the capillaries of the medulla, but by no means on account of their origin, or the structure of their walls.

Those arteriolæ rectæ, which in origin and structure are real arteries, are given off by the same branches of the renal artery, which also give off in the direction of the cortex the arteriæ interlobulares. The other arteriolæ rectæ possess no muscular rings, and are simply the greatly extended vasa efferentia of those glomeruli which lie nearest to the medulla. All the arteriolæ rectæ, whatever may be their origin, direct their course first towards the slit-shaped spaces which occur between the bundles of uriniferous tubules in the boundary region of the medulla.

Many of these little trunks, already before their entrance into the abovementioned spaces, break up into several small branches, and on reaching the spaces they continue to subdivide, but retain their course in the direc-

tion of the papillæ. In this way there is formed from the trunk of every arteriola recta a bundle of parallel arteries. Where this vascular bundle borders on the converging bundles of uriniferous tubules, the vessels break up into capillaries which entwine themselves about the uriniferous tubules like a network. Then, as the slit-shaped space is constantly growing narrower, first one artery and then another comes in contact with the tubules, and so they all, one after another, break up into capillaries. Hence in the direction of the papilla the number of the arteriolæ is constantly diminishing, until on arriving there only one or a few remain, which break up into capillaries in the papilla.

The capillary network surrounding the uriniferous tubules of the medulla is wide-meshed and inosculates with the vessels of the cortex, as has been already mentioned, at the boundary where the two regions border on each other.

In accordance with the arrangement just described, the supply of blood destined for the medulla is to a certain extent independent of that which goes to the cortex; for the former region could still be supplied with blood, even if the cortical arteries should be completely closed. On the other hand, the medulla is dependent on the stream through the cortex, since it must receive at least a part of the blood which flows down through the vasa efferentia of those glomeruli from which art. rect. originate. The blood which comes from the glomeruli is not always obliged, however, to take its course through the medulla, since it is not a rare occurrence for a vas efferens, from which arteriolæ rectæ originate, to send—previous to the commencement of these latter—to the convoluted tubules twigs which break up into capillaries in the same manner as occurs elsewhere in the cortex.

The veins of the medulla run in the same fissures which contain the arteries. The structure of their walls differs from that of other equally large veins in the fact that their endothelial cells are drawn out to an unusual length in the direction of the long axis of the vessel. This is so markedly the case in some instances that the walls appear as if woven out of fibres. As regards their course, the venulæ rectæ resemble the arteries of the same name, for the individual small trunks which result from the union of the capillaries of a small district do not at once unite with each other to form larger trunks, but remain independent as far as to the cortical end of the boundary region. Around the openings of the papillary ducts in the papilla there exists a small venous network, the chief part of whose blood escapes by way of the medulla; hence already in the papilla a few small venous trunks will be found commencing their upward course. As they proceed on their way through the fissure they are forthwith joined by others which have originated in the capillaries of the bundles of papillary uriniferous tubules; these are joined in turn by others which come from capillaries that lie a little higher up, etc. By receiving constant additions on their way from the papilla to the cortex, these veins at the cortical end of a fissure may reach the number of fifteen or even twenty (venulæ rectæ, fig. 172 vr).

Inasmuch as the veins exceed the arteries not only in number but also in diameter, the space which separates the bundles of uriniferous tubules in the medulla is therefore filled up chiefly by veins. Within the medullary region the individual veins which lie side by side in the same bundle very frequently anastomose with each other by loops. When the bundles arrive at the cortex the veins, which up to that point have remained isolated, rapidly unite into large trunks which pour their contents into the large veins of the cortex; the rule governing their arrangement is that for every

one of the bundles of uriniferous tubules surrounding a fissure: there will be a venous trunk which receives its supply from the small veins of the neighborhood, so that every bundle of veins discharges into the large venous branches of the immediate neighborhood, by at least so many small trunks as there are bundles of uriniferous tubules surrounding the fissure.

Concerning the relations of the blood-vessels to the uriniferous tubules of the medulla, there is yet to be mentioned that the veins which pass up through the axis of the fissure do not come in contact with the collecting tubes, and that the distance between them constantly increases, the nearer the veins approach the cortical boundary. Their relation, however, to the looped tubules is very different; the descending branches of the loops, on their way down from the region of the convoluted tubules to the bundles of straight medullary canals, pass through the midst of the bundles of veins in the upper portions of the boundary region.

Vessels of the Tendinous Capsule of the Kidney.—Over the surface of this tendinous membrane and within its substance there is distributed a wide-meshed capillary network such as is commonly seen in fasciæ. This network receives its supply in part from the few art. interlobulares which do not break up exclusively into the vasa afferentia of the glomeruli, and in part from the terminal branches of a few neighboring arterial trunks, such as the art. phrenica, lumbalis, suprarenalis. From the capillaries proceed veins which communicate in part with the stellate veins of the cortex, in part with other venous trunks, situated outside of the kidney. Every arterial branch coming from without is accompanied by two of these last-mentioned veins.

Lymph Vessels.—As is well known, larger and smaller trunks of lymph vessels come out not only from the hilus but also from the tendinous capsule of the kidney. Those coming out at the hilus can be followed along the larger trunks of the blood-vessels; nothing is known concerning their origin. The small trunks of the tendinous capsule originate, as we learn from a careful injection of the same, in a network of smaller lymph vessels which lie between the bundles of fibres of the tendinous membrane. If this network be injected, under even a moderate pressure, the material will pass on into the parenchyma of the kidney, and force its way into the spaces which separate the convoluted cortical tubules from each other. Just as easily, moreover, will the larger trunks in the hilus and the smaller ones of the capsule become injected if through a urinary stasis the spaces between the tubules should have become distended with fluid. This easy passage of fluids from one cavity to another necessitates the existence of certain anatomical arrangements; what these consist of, and whether they permanently or only at times favor the communication between the fissures and the lymph vessels, is unknown.

The *connective tissue* of the kidney is not everywhere of the same structure; the tendinous capsule and the immediate surroundings of the large blood-vessels in the papillary portion of the medulla are composed mostly of fibrillated connective tissue, while the labyrinth of the cortex and the boundary region of the medulla contain chiefly the cellular variety. The fibrous web, of which the tendinous capsule of the kidney is woven, is thickest on the free surface of the organ; from its deepest layers, those which are immediately next to the kidney, numerous but very delicate fibres dip down between the elementary tissues of the cortex. These and the communicating blood-vessels constitute the rather loose connection between the paren-

chyma of the kidney and the tendinous capsule. Between the convoluted tubules there is no fibrillated connective tissue. Leaving out of the question the outermost layers of the glomeruli, of which mention has already been made, the surroundings of these bodies, and especially of those which lie nearest to the medulla, form undoubtedly a very frequent exception to this rule; for around the glomeruli we often find a fibrillated connective tissue. Generally there will be found lying between the blood capillaries and uriniferous tubules of the labyrinth only a few small spindle-shaped cells, which are arranged with the long axis of their nuclei at right angles to that of the uriniferous tubules. These cells, however, do not in any way bind the convolutions of the uriniferous tubules to each other or to the blood-vessels, as may be ascertained by the inspection of a kidney which has been affected with acute œdema and urinary stasis. In such a kidney the cortical portion is considerably larger than that of its healthy neighbor, and consequently the convolutions of the tubules must have been considerably drawn out; in sections, moreover, it will be seen that there is quite a space between the blood capillaries and the uriniferous tubules. The spaces between the tubes of the medulla, in the immediate neighborhood of the papilla, are filled up with a distinctly fibrillated connective tissue, which surrounds the uriniferous tubules in a concentric manner. The farther one goes toward the boundary region, the more delicate becomes the fibrillated structure, and the more numerous appear the cellular elements, which from their spindle- or star-shaped bodies send out processes which are frequently of great length.

The nerves enter the kidney in company with the vascular trunks; throughout their course they are provided with but few ganglia. Anatomical investigations have not as yet afforded us any information concerning the termination of the nerves in the kidney. From the results of irritation we can conclude that they contain not only sensitive fibres, but also such as can shorten the ring-shaped muscles of the smaller arteries.

Historical.—Anatomy of the uriniferous tubules in the kidney of Mammals. The straight uriniferous tubes of the medulla have been known since the seventeenth century (Bellini); the convoluted tubules of the cortex since the middle of the last century (Ferrein). During the last thirty years our knowledge of the subject has been developed more rapidly by the help of the following methods:—

1. By comparison of the easily unravelled structure of the kidneys of the lower Vertebrates (Bdellostoma by J. Müller, Coluber by Bowmann) with those of Mammals.

2. By a more accurate adaptation of the artificial injections already before in use to the requirements of the kidney. First appears the application of atmospheric pressure (Huschke); then follows the employment of easily soluble substances (carmine and gelatine by Gerlach, glycerine and Berlin Blue by Henle); and finally the use of a pressure which can be accurately regulated, according to the time and strength required (C. Ludwig).

3. By the discovery of reagents which dissolve the connective tissue and blood-vessels, but leave the uriniferous tubules unaffected. Isaacs accomplished this object by boiling small pieces of kidney in very dilute sulphuric, phosphoric, chromic, boracic, tartaric, and citric acids, or even by boiling them in chloroform (?); Henle introduced the use of cold concentrated hydrochloric acid, and Schweigger-Seidel ascertained the best method of using it. C. Ludwig found it more advantageous to boil the pieces of

kidney in hydrochloric acid to which considerable alcohol had been added, and then to agitate them, for days if necessary, in distilled water.

4. By a more accurate comparison of the structure of the tubular walls in different parts of the same kidney (Henle). In this way it was ascertained—first, that the membranous covering of the glomerulus, discovered by J. Müller, is the blind termination of the uriniferous tubule, and is continuous at the neck with the convoluted tubule (Bowmann, Gerlach). Afterwards, Isaacs demonstrated the fact that at the boundary of the cortex the convoluted uriniferous tubule became narrower, and later Henle showed that after the entrance of this delicate canal into the medulla it bent round in the form of a loop; at the same time the same observer discovered that the broad canals, resulting from the subdivision of the papillary ducts, undergo further subdivision at the end of the medullary radius. The connection between the branches of the collecting tube and the ascending branch of the loop was established by C. Ludwig and Zawarykin. Finally, Schweigger-Seidel ascertained that the intercalated portion was a constant element in the course of the tubule.

The more accurate knowledge of the structure of the wall of the canal begins with Henle; he proved the existence of a basis membrane, of the opaque epithelium in the convoluted and of the hyaline epithelium in the straight tubules; Von Wittich ascertained the absence of the cell membrane in the epithelial cells of the convoluted tubules; Roth discovered that the capsules were composed of endothelial cells, and Steudener ascertained the peculiar shape of the epithelial cells in the ascending branch of the loop.

It became an easy matter to learn the distribution of most of the blood-vessels from the moment that gelatine was used in injections instead of the ordinary resin and wax mixtures. Only a few points offered any difficulties; as for instance the branches of the art. interlobulares, which pass between the glomeruli and pour their contents directly into the network surrounding the uriniferous tubules; Toynbee, Isaacs, and Schweigger-Seidel ascertained them to be regularly present in the kidney of Mammals. The arteriolæ rectæ veræ were discovered by R. M. Donnel and Virchow, independently of each other.

The fibrillated connective tissue of the medullary portion of the kidney is first mentioned by Goodsir; the cells peculiar to the cortical portion, by Beer and Schweigger-Seidel.

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CHAPTER XXII.

THE SUPRARENAL CAPSULES.

By C. J. EBERTH.

In Fishes the suprarenal capsules are small bodies, varying in size from the head of a pin to a lentil, and lying either on the anterior or the dorsal surface of the kidneys: there is either a single pair of them, or they occur in larger numbers. Leydig also reckons as suprarenal capsules those rounded bodies which envelop the vessels and sympathetic ganglia of the Selachia.

In the Batrachia—the caudate as well as the non-caudate—the suprarenal capsules consist of small, yellow granules, which are situated on the anterior surface of the kidney, upon the venæ renales revehentes.

In the Sauria the suprarenal capsules are yellowish bodies, lying upon the venæ renales revehentes, near where they empty into the lower vena cava. In Snakes they lie on the inner side of the sexual glands, upon the above-mentioned vein. The suprarenal capsules of the Chelonia occupy the same position as those of the Batrachia, while in Birds they lie at the upper border of the kidneys, immediately upon the vena cava.

Parenchyma.– The suprarenal capsules consist of two different masses of cells, called respectively cortical and medullary substances. This designation is appropriate for Mammals, inasmuch as it has reference to the relations between the two substances; but in the case of the other Vertebrates the terms are inappropriate, for the two substances do not occur in layers, but the cortical substance penetrates into the centre of the organ, while the mass of the medulla reaches even to the surface.

The suprarenal capsules of Fishes (Eel) are composed of rounded heaps of cells, which are angular and somewhat stellate in shape, and consist of either one or several layers. In the centre of these groups of cells there usually exists an irregularly shaped cavity.

It is yet to be ascertained whether the suprarenal capsules of Fishes possess any medullary substance.

In the suprarenal capsules of Batrachia, Sauria, Chelonia, and Birds, the cortical and medullary substances are not arranged in layers as in Mammals; both substances occur in the form of rounded heaps or branching trabeculæ and cylinders, which are mutually intermingled.

In the Batrachia the most superficial portions of the suprarenal capsules consist of solid rounded and oblong groups of polygonal cells, which are filled with oil-drops. These cells compose the cortical substance proper. The medullary substance, which is more feebly developed than in other animals, is represented here by only a few scattering polygonal cells and small groups of the same, collected around the cortical parts. In the deeper portions the cortical substance consists of branching and anastomosing cell-tra-

beculæ, which intersect with similar formations of medullary substance. The trabeculæ as well as the groups of cells possess no membrana propria.

Fig. 176.

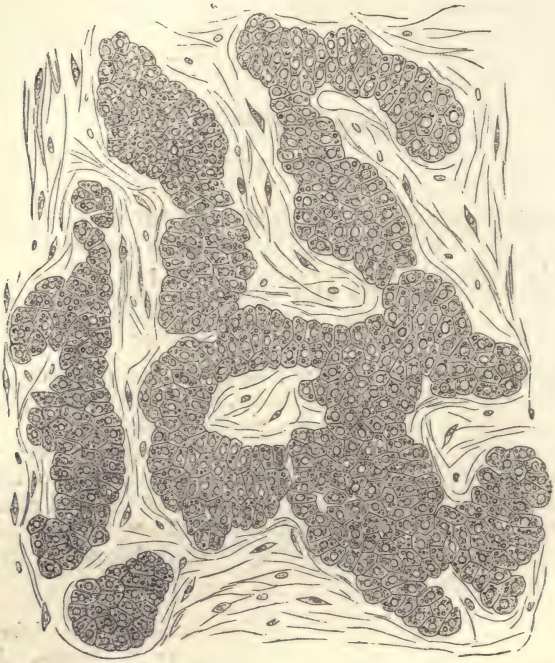

Fig. 176. Cellular groups and trabeculæ of the cortical substance, from the suprarenal capsule of the Frog.

In the Sauria and Chelonia the relations are similar.

The interweaving of the branching cortical and medullary trabeculæ is still more pronounced in Birds. In the place of the solid trabeculæ, cylindrical tubes with a narrow calibre are sometimes met with: these tubes, like those of cold-blooded animals, do not form a continuous network, but frequently terminate blind. In the cortical portions the cells of these tubes are narrow cylinders with eccentric nuclei, while in the medullary parts they are polymorphous elements—mostly cylindrical and polygonal.

In Mammals the two substances are arranged in layers. The external or cortical substance is of a grayish yellow, or, if very rich in fat, of a whitish yellow color; when broken the fractured surface appears radiated. The cortical surrounds like a capsule the inner, gray medullary substance. Sometimes small portions of the cortex penetrate into the substance of the medulla in company with the larger vessels. In the narrow borders there is no medullary substance; the innermost cortical layers of both sides come into direct contact here and form a simple brownish band.

The accessory suprarenal capsules, a large number of which may often be seen as small yellow granules on the surface of the principal organ, are partially detached portions of the cortex, in the centre of each of which exists a very vascular connective tissue.

In Man the innermost cortical layer is found in a softened condition through putrefaction. In that case there will be seen between the cortex and the medulla a cavity which is filled with a brown pulpy material consisting of blood and degenerated cortical substance.

In the cortex two or three layers may be distinguished.

Where there are three, then the outer and inner layers, consisting of rounded groups of cells (parenchymal bodies), are separated by a layer of cylindrical cell-trabeculæ (cortical cylinders, cortical trabeculæ). This is the case in Man, the Hog, Dog, Hedgehog, and Guinea-pig.

Fig. 177.

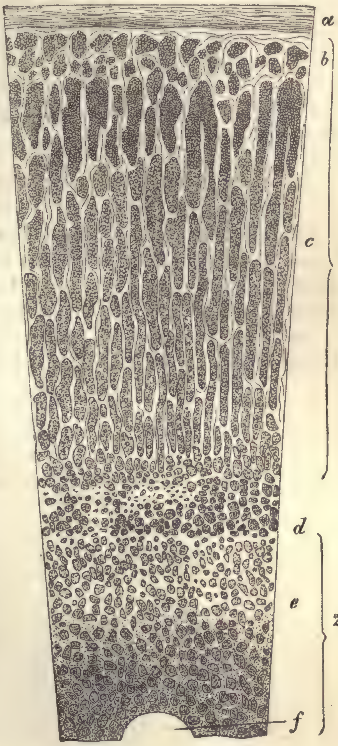

Fig. 177. Perpendicular section through the suprarenal capsule of Man. 1, cortex; 2, medulla; *a*, capsule; *b*, layer of outer cell-groups; *c*, layer of cell-trabeculæ (Zona fasciculata); *d*, layer of inner cell-groups; *e*, medullary substance; *f*, transverse section of a vein.

In other animals the outer groups of cells are wanting: the cortical cylinders come into direct contact with the investing capsule, and pass continuously on the inner side into the layer of inner cell-groups. (Cow, Horse, Cat, Rabbit, Mouse.)

These different layers, however, are not separated by such sharp limits as exist between the cortical and medullary substances. While in the first group of animals, particularly in Man, the outermost layer is separated quite distinctly from the middle layer, the boundary between the latter and the inner layer is quite indistinct.

The outer, like the inner cell-groups, consist of polygonal and rounded masses of protoplasma, containing a single nucleus, and arranged either singly or in groups. In the Cow the innermost layer seems to be a pretty uniform infiltration of the stroma with polygonal cells. In many animals (Man and Rabbit) the separate cells often unite together into a single mass. In the Dog the outer cell-groups, which consist of cylindrical cells, are either oblong in shape, or they resemble a horse-shoe.

The cortical trabeculæ consist of oblong cylindrical masses of cells, which are so closely packed together as to give to the cortex—in somewhat thick sections, and under a small magnifying power—the appearance of being entirely composed of long, parallel trabeculæ (Man). Beneath the capsule many of the trabeculæ communicate with each by short loops (Man). They also sometimes anastomose elsewhere in their course.

The cellular elements are the same as those in the outermost layer, with the exception that here they contain larger and smaller oil-drops; in Man this is only sometimes the case, but in many animals these oil-drops are constantly present.

The innermost cells of the inner cortical layer in Man are characterized by their yellow color.

Fig. 178.

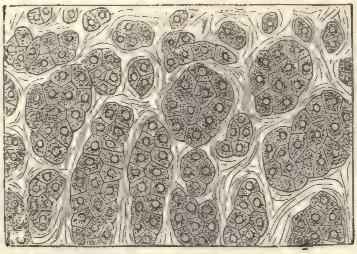

Fig. 178. Single cells and cell-groups of the outermost cortical layer; from the Human suprarenal capsule.

In those animals which possess no outer cell-groups, the superficial cortical trabeculæ consist either of shorter, rounded and cylindrical masses (Cow), which often anastomose with one another; or else of cylinders, which beneath the capsule communicate with each other by means of short arches (Rabbit, Mouse, Cat). In the Horse the cortical trabeculæ are narrow bands and troughs, which, in the direction of the periphery of the organ, become converted, by the gradual union of their borders, into hollow cylinders with blind terminations (Kölliker, Eberth).

Fig. 179.

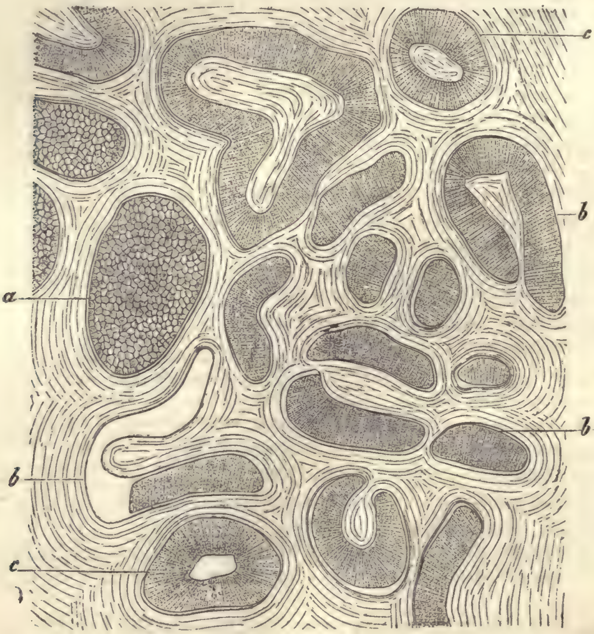

Fig. 179. Horizontal section through the outermost cortical portions of the suprarenal capsule of the Horse. *a*, blind termination of a cylinder; *b*, groove-shaped and cylindrical cortical trabeculæ; *c*, stroma.

In the Cow the cells of the cortical trabeculæ are somewhat cylindrical in shape, or else polygonal: in the former case their long diameter stands at right angles to the radius of the trabecula. In the Rabbit the cells are polygonal, and in the Horse they are narrow cylinders.

In Man, as well as in other animals, irregularly-shaped fissures are often found in the centre of the rounded or cylindrical cell-groups. As to the epithelium-lined vesicles described by Grandry I have never yet met with them.

Fig. 180.

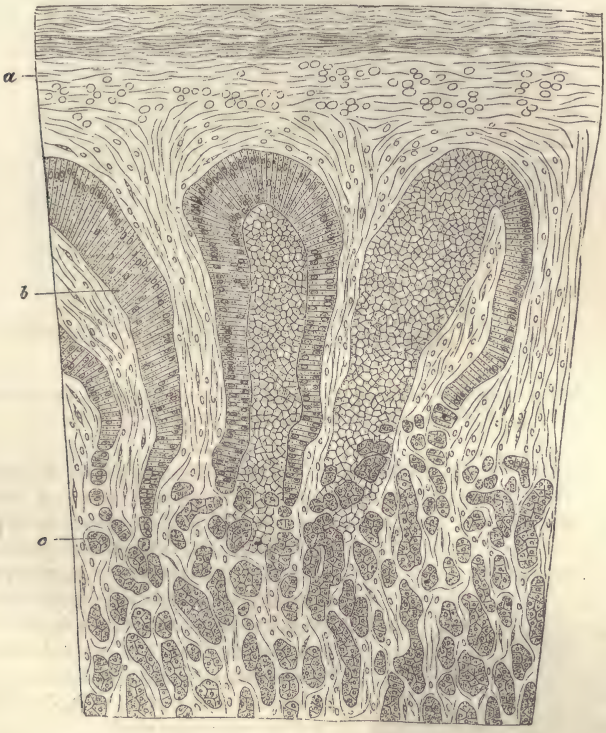

Fig. 180. Vertical section through the cortical portion of the suprarenal capsule of the Horse. *a*, capsule; *b*, cell-trabeculæ; *c*, cell-groups.

Medulla.—Between the broad, narrow-meshed vessels of the medulla lies a spongy tissue which is composed of a delicate connective substance that gives support to the medullary cells. These last occur either isolated or, more frequently, in rounded groups (Man); sometimes they form plexiform trabeculæ (Cow, Horse, Pig, Dog, Cat, Rabbit, Guinea-pig, Mouse, Hedgehog). From these trabeculæ outrunners sometimes penetrate into the cortex: small masses of the medullary substance may even be found near the surface of the organ.

The cells of the medullary portion are of a delicate consistency and exceedingly variable in shape. In Man they are stellate and polygonal; in the Pig, often cylindrical; whereas in the Horse and Cow their shape is at times scarcely recognizable; in their place we find a finely granular mass

with central or eccentric nuclei, and sometimes cylindrical and anastomosing stellate cells are intermingled with the mass.

Fig. 181.

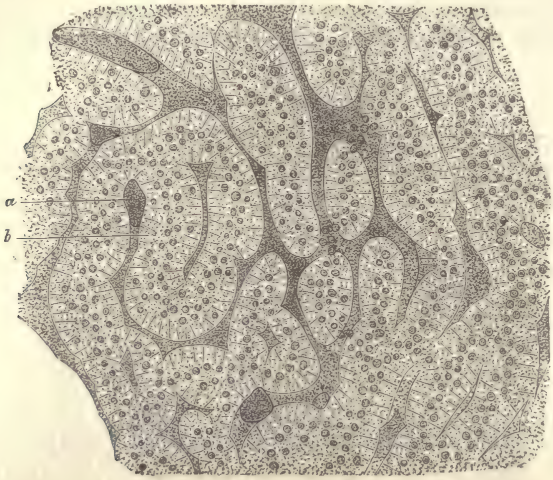

Fig. 181. Vertical section through the medullary substance of the suprarenal capsule of the Cow. *a*, blood-vessels; *b*, trabeculæ of medullary cells.

In solutions of the Bichromate of Potassa the medullary cells assume an intensely yellow or brown color, while the cortical portion remains unchanged, or at the very most takes on a feebly yellow tinge, as other tissues do. This reaction, which manifests itself with equal intensity in a great variety of animals, is prevented by alcohol. It affords valuable assistance in distinguishing the cortical from the central cells in places where the two substances cannot possibly be recognized apart, either by their form or their arrangement.

Fig. 182.

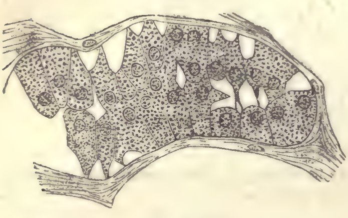

Fig. 182. Trabeculæ of medullary cells from the suprarenal capsule of the Cow.

In Man the reaction which follows is brown, but it is very light compared with the intense coloring produced in the Cow, Pig, Dog, Cat, Hedgehog, Guinea-pig, Rabbit, Mouse, Rat, Dove, Duck, Fowl, Turtle, Lizard, Frog, and Salamander. Unfortunately, the only specimens of the suprarenal capsules of Fishes at my disposal were such as had been preserved in alcohol.

Framework. From the connective-tissue capsule coarser processes penetrate into the depths of the parenchyma and subdivide it into territories (Cow). From these more delicate bands of connective tissue are given off laterally which anastomose with one another. Between these trabeculæ rounded and oblong spaces are left, which are filled with the cell-groups and trabeculæ.

In the Cow the coarser bands of connective tissue soon break up into a very delicate framework, with uniformly large, angular meshes, each of which contains a cell.

Fig. 183.

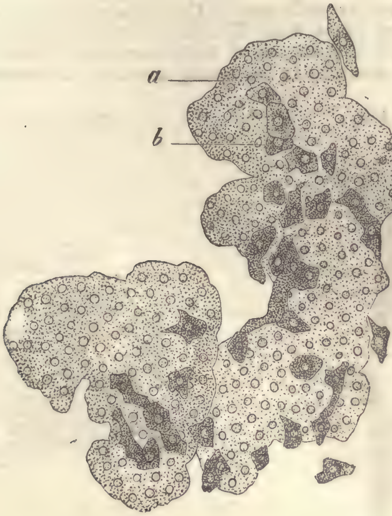

Fig. 183. From the suprarenal capsule of the Frog. *a*, agglomeration of cortical cells; *b*, medullary cells.

In the medullary portion the stroma is more scanty than in the cortex. It only serves in that locality as an investment around the cell-groups.

Grandry, Henle, and others assert that the cell-groups of the cortex and medulla are surrounded by real membranes, but I have not been able to find any such, not even after maceration in acids and alkalies. Perhaps the delicate, membranous connective-tissue septa, or the walls of blood-vessels, which often lie in immediate contact with the cell-groups, have been mistaken for the membranes of these latter.

Blood and Lymph Vessels.—The suprarenal capsules are among the most vascular organs. They receive their blood from the Arteriæ phrenica, cœliaca, Aorta and renalis. A few branches of these vessels traverse the capsule and penetrate with its offshoots into the central medullary mass, while others break up already in the capsule into a broad-meshed capillary network; others still, after penetrating the capsule and breaking up into smaller twigs, pour their contents directly into the capillaries of the cortex.

The veins originate in the medulla and empty into the large central vein, which comes out from the organ at the hilus and pours its contents into the vena cava inferior. Small veins accompany the arteries in pairs through the cortex and empty into the Venæ phrenicæ, renales, and Cava inferior. According to Arnold they originate in the middle cortical layer (Zona fasciculata).

In the outermost cortical layer the arteries break up into a capillary

network whose rounded meshes contain the cell-groups (Parenchymal bodies). In the second zone these vessels form meshes which are arranged in a radiating manner and communicate with each other by short transverse anastomoses: in the innermost layer they are again arranged as in the outer layer.

Arnold makes out vascular coils even in the outermost cortical layer. I have not been able, however, any more than Kölliker, to persuade myself that they occur there. The variableness in structure of the cortex would, however, readily account for a certain degree of diversity in the arrangement of the vessels.

Fig. 184.

Fig. 185.

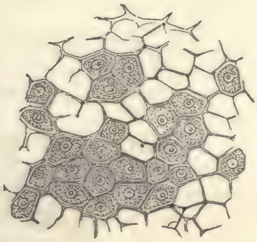

Fig. 184. *a*, connective-tissue bands of the outermost cortical layer; from the suprarenal capsule of the Ox. *b*, parenchyma cells.

Fig. 185. Delicate framework from the innermost cortical layer of the suprarenal capsule of the Ox, with a few parenchyma cells.

The medullary vessels originate in the capillaries of the innermost cortical layer. They constitute a narrow-meshed network of irregularly broad, frequently much dilated vessels, which pour their blood into the renal vein. The central portions of the medulla, according to Arnold, are also fed by arteries, which follow the course of the connective-tissue bands and communicate with the capillaries of the medulla.

The narrower cortical capillaries and the broad ones of the medulla are canals with very thin walls, composed exclusively of the tubular endothelium. They lie in immediate contact with the parenchymal bodies, and are so firmly attached to the scanty stroma that it is with difficulty that we can obtain them in an isolated condition. This condition of things led to the supposition that the blood travelled here through ways which were not provided with special walls.

Lymph Vessels.—Besides the few small trunks seen on the surface of the organ by Ecker, Kölliker, and Arnold, the last-named authority mentions also deep-seated lymph vessels. The thin-walled, sinuated spaces, which Moers observed by the side of the arteries in the substance of the gland, were considered by him as sections of lymph tubes.

Nerves.—The suprarenal capsules are rich in nerves. These come from the Ganglion semilunare, the Plexus renalis, the Phrenicus and the Vagus, and enter the organ at its inner and lower border. They ramify chiefly throughout the medullary substance, where they appear in the form of intercrossing broad bands, or, more rarely, as delicate plexuses. Bi- and multi-polar ganglia are frequently met with, either isolated or in larger groups along the medullated nerves, at their points of bifurcation (Holm, Eberth). Ganglion cells are of rarer occurrence in the cortex. The nerves consist of narrow fibres with dark borders.

It is still a matter of doubt whether the nerves terminate in the substance of the organ, or simply traverse it as an endless plexus.

It is improbable that those cells, which in the Ox are found at the boundary between the cortex and the medulla, and in the latter region accompany the nerves in groups, possess a nervous nature. These elements are smaller than the true ganglion cells, though somewhat larger and more brilliant than the cells of the cortex: they are angular and possess no outrunners. They are colored somewhat more rapidly by carmine than the cortical cells (Holm, Eberth), and are not, like the medullary cells, rendered brown by the Bichromate of potassa. In their arrangement they resemble most those elements of the cortex which in rather broad groups accompany the larger vessels through the medulla (Holm, Eberth).

In the Lizard and the Batrachia I can find no nerves in the parenchyma; in the Turtle they are very few. In Birds large ganglia are found on the surface of the organ, while in its interior there are but few nerves and ganglion cells. Among Mammals the suprarenal capsules of the Carnivora and of the Rabbit possess but few nerves, while those of Man and the Pig are very rich in nerves: this is especially true of the Cow, where they are very abundant.

After the statement, that the medullary substance of the suprarenal capsules consisted entirely or chiefly of ganglion cells (Luschka, Leydig), was proved to be incorrect, it became necessary to investigate anew whether, as Leydig maintains, in the Selachia, Ganoids, and Reptiles, "portions of the suprarenal capsules are attached to the individual ganglia of the Sympathetic, or rather whether they do not constitute integral portions of these ganglia." These portions of the Sympathetic ganglia, it is supposed, correspond to the medullary substance, while the cortex on the other hand seems, in Fishes and Reptiles, to be accumulated around the vessels. The so-called axillary hearts in the Torpedo would represent such cortical portions.

Leydig is also disposed to consider as equivalents of the suprarenal capsules the groups of cells which in Invertebrates (Paludina, Pontobdella) are found alongside of the ganglia.

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CHAPTER XXIII.

THE URINARY BLADDER AND THE URETERS.

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OF THE PHYSIOLOGICAL INSTITUTE OF THE VIENNA UNIVERSITY.

The urinary bladder and the ureters constitute a complex organ, to which is assigned a rôle more passive than active, the physiological significance of which is, in all probability, that they shall receive and dispose of the urine excreted by the kidneys.

This accounts for their relative anatomical simplicity, as well as for the similarity which is found in their construction.

The bladder is covered externally by the peritoneum, which extends farther downwards on the posterior wall than it does in front, or at the sides. The thickness of the walls of the bladder changes according to the amount of distention of the organ, and varies in Man, if we exclude local differences, from 2 to 15 millim.

The urinary bladder of most Mammals is similar in construction to that of Man; I will therefore restrict myself to a description of the latter.

Among the Vertebrates the bladder is absent in Birds, certain Fishes, Amphibia, and Reptiles. The urine of these animals is so rich in urates, that too heavy sedimentation would occur if it were retained for any length of time in a vesical cavity.

The urinary bladder of some Reptiles and Amphibia (for example the Turtle, Frog) empties, like the ureters, into the cloaca, so that the urine can be voided without having passed through the bladder. A similar arrangement exists among Mammals in the Monotremata.

In the Human bladder the following coats are encountered from within outwards.

I. The Epithelium.—This layer is subdivided into several strata, characterized by the greatest differences.

Most internally are found one or two layers of cells of a polyhedral form. These are for the most part rounded, or, especially the larger ones, rather flattened, and vary greatly in shape and in size. Their borders and angles are often drawn out in such a way that a concavity is formed on their under surface, into which the body of a cell of the second layer fits. Their contents are moderately granular and display one or two nuclei with distinct nucleoli. These correspond to the cells, which are frequently found in urine after it has been voided. Sometimes there may be observed very delicate hyaline drops, which come out from the sides of the cluster of cells under examination, without causing any shrinkage or apparent change in the cells themselves,—as is also seen in examining epithelium from other parts.

The next layer of epithelial cells (fig. 186. *a*, *c*, 2) is readily distinguishable from the others by the regularity of its elements, which are arranged in a more simple manner. The cells of this younger layer are equal in size

(about 0.03 millim. in their longest diameter), and so arranged that their broad convex bases are turned towards the surface, while their points dip down into the lowest stratum of cells. These smaller ends are prolonged into undivided points, of variable lengths and often varicose; their appearance reminds one very much of the epithelial cells of the mucous membrane of the nose.

Fig. 186.

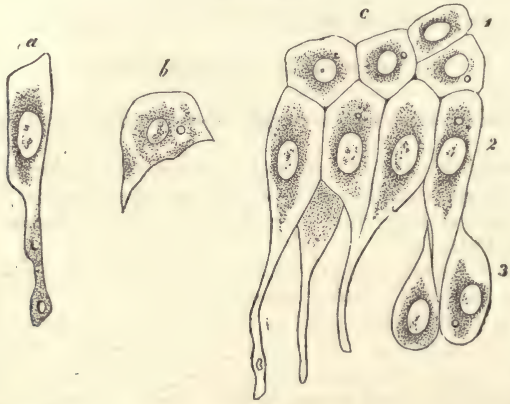

Fig. 186. Epithelium of the urinary bladder. *a*, a cell of the second layer; *b*, a cell of the first layer; *c* shows the 1st, 2d, and 3d layers of the epithelium in connection.

The ultimate disposition of these pointed extremities of the cells, which extend down into the lowest layer of the epithelium, cannot be readily determined; still it seems very probable that they form a connection with the superficial layer of the connective tissue upon which the bladder epithelium rests, either with the connective tissue itself, or with the nervous elements of that layer. In favor of this hypothesis is the circumstance, that these cell-prolongations, no matter with how much care they may be isolated, never continue on to a free pointed extremity, but on the contrary always have an appearance as if they did not possess their entire length, but had been merely torn off. Furthermore, after a separation of the epithelium, there may be often observed fine bent filaments projecting out from the connective tissue, having the same size as the prolonged extremities of the cells before mentioned; and it is even possible, under favorable circumstances, to obtain views of specimens which seem to indicate a previous connection between the two ends.

The question, so much discussed, of the origin of epithelial cells from the underlying connective tissue would go to substantiate the inference to be drawn from the appearances above detailed.

The deepest and most external layer of the epithelium (fig. 186. *c*. 3) is composed of irregular oval cells, which are often drawn out toward the surface of the membrane, wedged in between the conical ends of the cells of the middle layer.

II. The Connective-Tissue Layer.—A layer of very dense connective tissue, about 0.02 millim. thick, rich in nuclei and composed of fine fibres, lies next to the epithelium and is sharply separated from the outer layer of

the connective-tissue coat, which outer layer is from 0.8 to 1.5 millim. thick, poorer in nuclei and composed of thick bundles of fibres. Much elastic tissue and many smooth muscular fibres—sometimes single, sometimes arranged in bundles—are scattered through the latter in various directions.

Single acinous glands, similar to those of the Pars prostatica urethræ, are found near the urethral opening. They are by no means constant and appear to be very sparingly present during the first years of life, which would point to a new formation of these glands at a period somewhat removed from birth. The distribution of the nerves and vessels will be described further on.

III. The Muscular Layer.—The fibres of the muscular coat are from 0.1 to 0.25 millim. long and possess distinct nuclei, long drawn out and staff-like in appearance. The muscular fibres of the urinary bladder of the Frog are considerably longer (0.4 millim. and over) than those of Man, and are very perfectly isolated.

The muscular fibres of the Human bladder are grouped together into rounded bundles from 0.03 to 0.15 millim. thick. These are separated by connective tissue, containing the vessels and nerves. The thickness of this enveloping connective tissue varies greatly, but usually it is relatively more considerable in children than in adults; indeed, in the former, the amount of the connective tissue of the muscular coat often equals that of the muscular tissue itself, and may even surpass it.

In the neighborhood of the Sphincter vesicæ the bundles of muscular fibres are separated and broken up by the interstitial connective tissue in such a way, that the ultimate fibres become isolated and are found either single or in very small groups.

The course of these muscular fasciculi is by no means regular, but deviates greatly in individual cases from any diagrammatic representation which might be offered.

The following description will give an idea of their course, at once simple and yet as near the exact truth as possible. The innermost layer is constituted by circular fasciculi, which cross each other at acute angles, forming a network with oblique meshes. The muscular fibres of this layer are particularly well developed around the internal orifice of the urethra. At this point the arrangement of the fasciculi is more regular. They run nearly parallel to each other, so as to form a complete ring around the orifice of the bladder, the Sphincter vesicæ. Outside of this circular layer come the longitudinal fasciculi, which become more plentiful toward the vertex, and are continued, in Children, upon the obliterated (or it may be still partially patulous) urachus. It is impossible to undertake a more detailed account of the course followed by the muscular fibres, since I have found the same to vary so much in all the bladders I have examined, that any thorough description would only be correct for a single case.

The Trigonum Lieutodii consists merely in a thickening of the connective-tissue layer, with all its elements, from the orifices of the ureters to the Caput gallinaginis.

The arteries of the bladder (superior and inferior vesical branches of the Hypogastric) encounter the bladder at its posterior wall and are distributed to the fundus. They penetrate the muscular coats, in which some small branches are given off, and finally terminate in the connective tissue, about midway between the epithelium and the muscular coat (or, indeed, nearer the former), by branches running parallel to the surface. From these stems still smaller branches rise towards the epithelium, immediately beneath which,

and separated by a hardly appreciable layer of fibres, they form a fine dense capillary network. When the bladder falls into folds these little branches occupy the middle portion of the fold, and in this way are shielded from injury; the nerves, still as medullated fibres, can be followed into the connective-tissue layer. They are seen to best advantage near the neck of the bladder, where they are most abundant. It is difficult to determine their mode of termination accurately. Kisselew states that they terminate in certain of the epithelial cells, which are distinguishable from the other cells of that layer from the fact that they imbibe carmine more readily and adhere more strongly to the underlying connective tissue. It is probable that he saw objects similar to the wandering cells.

A few ganglion cells are found, sparingly scattered along the course of the nerves.

In the bladder of the Frog the medullated nerve fibres offer particularly fine subjects for investigation. In their meshes they enclose the large ganglion cells, pigmented in yellow and provided with an epithelial layer, which Jakubovitsch first described.

The Ureters—as has been previously stated—show a construction exactly like that of the bladder. The epithelium is precisely similar to that of the bladder; under it comes a layer of connective tissue and then a triple layer of muscular tissue, of which the innermost is directed longitudinally, the middle is circular, while the outermost, which is the weakest, has a less regular direction, although it tends to be also longitudinal; a thin layer of connective tissue (as adventitia) constitutes the outermost stratum of the ureters.

The blood-vessels are distributed in a manner analogous to those of the bladder. Engelmann * describes them, in the Rabbit, as a sub-epithelial capillary plexus, upon which the epithelium is situated, unseparated by any layer of connective tissue. The position of the capillary plexus in Man, however, seems to be more protected and less superficial.

A small number of medullated nerves make their way into the substance of the ureter. I have not been able to demonstrate the existence of ganglion cells except in that plexus of nerves found in the adventitia, which has been named by Engelmann Basis-plexus (Grundplexus).

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CHAPTER XXIV.

THE TESTICLE.

By VON LA VALETTE ST. GEORGE.

Outer Tunics of the Testicle.—The testicle in Man is closely surrounded by a dense fibrous envelope, the Tunica albuginea, which is continued over the upper part of the Epididymis.

The free surface of this fibrous investment is covered over by the inner or visceral layer of the Tunica vaginalis propria. Hence it is smooth and shining.

This visceral layer of the Tunica vaginalis propria (the Tunica adnata) is inseparably united with the Albuginea over the surface of the testicle; over the epididymis, on the contrary, it is but loosely attached. The tissue of this serous covering is frequently lengthened out into tufted excrescences, which are found both at the sharp edge of the Epididymis and upon the upper part of the testicle. They have been exhaustively described by v. Luschka.* These excrescences are covered by a flattened epithelium in several layers, or merely by round cells arranged singly. Cells have also been observed which offer an irregular form and show constrictions.

Fig. 187.

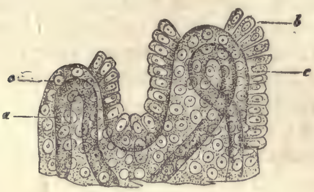

Fig. 187. Excrescence of Tunica vaginalis with cylindrical epithelium. *a*, vascular loop; *b*, epithelium; *c*, nuclei.

Fig. 188.

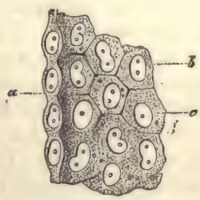

Fig. 188. Epithelium of the Tunica albuginea. *a*, border tilted up; *b*, cells; *c*, nuclei.

I have often seen these excrescences as much as 7 millim. long and 4 mm. broad, and among them some which were covered by cylindrical cells.

Elsewhere upon the Tunica adnata the epithelium, which may be easily obtained by scraping the surface, consists of a layer of polyhedral cells of different sizes, with sharply defined, oval nuclei, and one or two nucleoli. The contents of the cells are finely granular, and sometimes contain little fatty granules. On the head of the Epididymis and upper part of the testicle are situated the so-called Hydatids of Morgagni, of which the upper—either hollow or solid, and more or less pediculated—is considered as the remains of Müller's duct, while the lower, flattened out and club-shaped, some-

* Virchow's *Archiv*, Bd. vi., S. 321.

times communicates, according to v. Luschka,* with the canal of the epididymis. A convolution of closed tubules, distended at each end into a clubbed shape, may be found lying between the head of the epididymis and the Vas deferens. It has been named Corpus innominatum, Parepididymis, Organ of Giraldès by Giraldès,† Henle,‡ and Kolliker § respectively. It is probably the remains of the Wolffian body—an analogue ot the Parovarium.

The fibrous covering of the Testicle is composed of connective tissue with a few fine elastic fibres. Its thickness increases towards the posterior border of the testicle. Here, under the name of Mediastinum testis or Corpus Highmori it passes to the inside of the gland. Moreover it sends into the gland from its entire under surface—besides scattered bundles of connective-tissue fibres—the flat processes, known as the Septula testis, which are directed toward the Mediastinum.

The parietal layer of the Tunica vaginalis propria, like the visceral, is composed of connective tissue, traversed by fine elastic fibres and covered on its inner surface by the same simple flattened epithelium.

The Tunica vaginalis propria is covered by a second layer of connective tissue, the Tunica vaginalis communis, which, above, is only a loose laminated structure, but becomes more dense towards the point of the testicle.

On the inner side of this Tunic, between it and the Tunica propria, unstriped muscular fibres were found by Kölliker. These have been described by Henle as Cremaster internus. According to Rouget, these fibres are also prolonged upon the Septula testis.‖ The muscular fasciculi of the Cremaster externus, surrounded by a network of elastic fibres, are spread over the surface of this Tunica communis. There are found upon the surface also, according to Rektorzik,¶ little rounded, partly pediculated excrescences without vessels. The outermost coverings of the testicles are furnished by the Scrotum. The subcutaneous connective tissue of the scrotum contains numerous smooth muscular fibres, arranged singly as well as in a network of continuous fasciculi. These little muscles, according to Treitz,** are connected by elastic tendons to the fore part of the pubic bones, the Ligamentum suspensorium penis and the Fasciæ latæ. This Tunica dartos, whose true structure was first described by Kölliker, is attached to the Tunica vaginalis communis by a loose connective tissue, in which, posteriorly, there is a layer of fat cells.†† The Dartos forms the Septum scroti, which divides the cavity of the scrotum into two halves. The scrotum is provided with a darkly pigmented skin, containing sweat and sebaceous glands of large size.

The Internal Parts of the Testicle.

Structure of the Seminal Tubules.—The Septula testis partition off the testicle, separating the true glandular substance into the lobuli testis.

The glandular substance consists mainly of the little canals of the testicle, the Canaliculi seminales, which are convoluted in an intricate manner, anastomose with each other near the surface of the organ, and finally are all

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* Virchow's *Archiv*, Bd. vi., S. 310.

† *Bulletin d. l. s. anat. de Paris*, 1857, p. 789. *Journal de la Physique*, iv. p. 1.

‡ *Handbuch der Eingeweidel.* S. 364.

§ *Handbuch d. Gewebel.* S. 537.

‖ *Compt. rend.*, t. 4. p, 902.

¶ *Wiener Sitzungsberichte*, 1857. Jan. S. 154.

** *Prager Vierteljahrsschrift*, 1853, 1, S. 113.

†† Henle, *Handbuch der Eingeweidelehre*, S. 420.

directed towards the Mediastinum. These canals finally become more straight; several of them unite, and they sink into the Corpus Highmori and are continued on to run together and form the Rete testis. Out of the upper part of the Rete emerge from twelve to fourteen tubules, which again become convoluted into conically shaped masses, Coni vasculosi, and constitute the head of the epididymis. They empty one after the other into the canal of the epididymis.

This latter, which is also much convoluted, lies along the posterior border of the testicle, and gives off a branch ending in a blind extremity called Vas aberrans. It finally separates from the testicle and mounts up, at first still a little wavy and then perfectly straight, under the name of Vas deferens.

As to the manner in which the canaliculi commence, the majority of authors (J. Müller, Krause, Berres, Beale, Sappey, Kölliker, v. Luschka) agree that they originate partly in blind ends and partly by anastomoses. I have frequently found offshoots with rounded (blind) extremities among the Tubuli seminiferi of a child, which had been macerated in vinegar.

The seminal tubules measure 0.2 millim. The thickness of their walls varies with the amount of distention.

Various descriptions have been given of this membrane, which forms the wall of the tube. According to the older statements of Henle,* which hold good, as he supposes,† for the smaller Mammals, it is clear and structureless, and contains a few long oval nuclei. Lereboullet ‡ states that it is structureless in the Rabbit. Valentin § held that a middle muscular layer could be demonstrated, covered internally by pavement epithelium, and bounded externally by a clear transparent membrane containing oval cell-nuclei. Gerlach ‖ finds a difference between the structure of the seminal canals in newly born and young animals from that of adults. While in the former the walls of the Canaliculi are composed of a structureless membrane as clear as glass, containing few or many oval cell-nuclei, in the latter he found externally a layer of connective-tissue fibres, containing a few oval nuclei. Henle¶ describes the membrane of the seminal canals as follows:—"It appears marked longitudinally, upon a longitudinal section; concentrically, upon a transverse section. In both sections, dark, seemingly rod-like nuclei are seen between the markings. When spread out and viewed from the surface, it appears homogeneous, with pale circular nuclei, arranged in quite a regular manner. Hence we may conclude that it is lamellar, and constructed out of flat scales with flattened nuclei."

Fig. 189.

Fig. 189. Seminal tubules with blind ends, from a child one year old.

Frey ** distinguishes two layers, the one a structureless Membrana propria, and the other, external to it, a thick covering of a striped fibrous nature, with oval nuclei. He gives a plate from the testicle of the Calf as well as a representation of Human seminal canals.

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* *Allgemeine Anatomie*, S. 926.
† *Handbuch der Eingeweidelehre*, S. 354.
‡ *N. A. Acad. Nat. Cur.*, xxiii. 10.
§ *Handwörterbuch der Physiologie*, v. R. Wagner, Bd. i., S. 785.
‖ *Handbuch der Gewebelehre*, S. 367.
¶ *Handbuch der Eingeweidelehre*, S. 353.
** *Handbuch der Histologie*, S. 607.

According to von Hessling * the seminal canals are composed of a structureless glandular membrane, Membrana propria (1 μ † thick), outside of which lies a sheath of lamellar, finely striped connective tissue, 3 μ thick, furnished with long oval nuclei and sharply separated from the remaining interstitial connective tissue.

Kölliker ‡ styles the enveloping membrane of the seminal tubules a fibrous tunic, and states that a lining Membrana propria on the inner side of the same may be easily demonstrated with caustic potash.

Letzerich § gives the Rabbit a structureless membrane furnished with pale, elliptical nuclei.

I myself, in a Child one year old, after maceration of the testicle in vinegar, found the contents of the seminal canals surrounded by a very fine, structureless membrane, outside of which was an Adventitia rich in nuclei.

The seminal tubules of an eight-inch embryo taken from a Cow, as well as those taken from the testicle of a Calf, showed a rather thick structureless Propria, and a thin Adventitia containing nuclei.

In Dogs, Guinea-pigs, and Rabbits two layers are always distinguishable.

On the other hand in the seminal tubules of adult Men I could only distinguish one membrane, such as has been thoroughly and exhaustively described by Henle.

Embedded between the seminal tubules in the interstitial connective tissue the peculiar clusters of cells are found, which were first described by

Fig. 190.

Fig. 190. Portion of a seminal tubule of an embryo taken from the Cow. *a*, adventitia; *b*, propria.

Fig. 191.

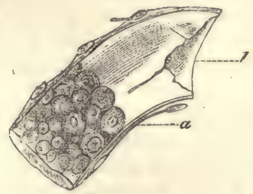

Fig. 191. Portion of a seminal tubule from the Calf. *a*, adventitia; *b*, propria.

Kölliker, ‖ and are to be counted among the ordinary connective-tissue cells.¶

Leydig ** also speaks at length on this point, and considers it to be the common arrangement in Mammals, that the connective tissue uniting the seminal tubules should contain a cell-like mass, which, when present only in small quantities, follows the course of the blood-vessels, but on the other hand embeds the seminal tubules entirely, where it is extensively present. In the Boar it reaches such an extreme development that a section of the testicle presents a chocolate-colored appearance. The same holds good with the Horse, and is also observed in the Lizard.

* *Grundzüge der Gewebelehre*, S. 328.
† Micromillimetre.—*Translator's note.*
‡ *Handbuch der Gewebelehre*, S. 521.
§ Virchow's *Archiv*, Bd. xlii., S. 570.
‖ *Mikroskopische Anatomie*, ii. 2, S. 392.
¶ *Handbuch der Gewebelehre*, S. 524.
** *Lehrbuch der Histologie*, S. 594.

Henle * has thoroughly investigated these interstitial collections of cells and illustrated them by figures. They consist, according to him, of a finely granular substance, not unlike the contents of ganglion cells, and sprinkled with nuclei, which are easily distinguishable from the nuclei of the contents of the seminal tubules, by their similarity of form, their smaller size ($3\,\mu$), their globular shape, and central nucleoli, which are everywhere visible. Henle considers them an essential constituent of the gland, although he is unable to attribute to them any share in its function.

It is easy to demonstrate th accuracy of the above descriptions. The role of these clusters of cells remains problematical.

After the seminal tubules have entered into the mediastinum testis, they lose their own special walls and pass on into the more or less wide, irregular cavities of the Rete testis.

The Vasa efferentia are thicker (0.6–0.4 millim.) than the seminal tubules, since a considerable layer of unstriped muscular tissue is added to their walls.

The Cellular Contents of the Seminal Tubules.—The outermost layer of the cells forming the contents of the seminal tubules has indeed also been styled the epithelium of the tube. If I fail to indorse this positively, still I can make out a peculiar form in the cells of this outer zone. According to a notice by Kölliker,† Sertoli describes these cells as possessing processes and closely connected with each other. His preparations were made by treating the testicle with a solution of sublimate, at 0.5 per cent. strength, and subsequent maceration in water. Unfortunately Sertoli's

Fig. 192.

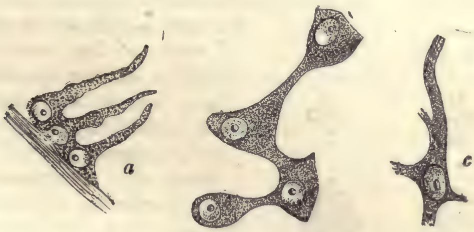

Fig. 192. Cells of the outer zone from the seminal tubules of the Steer, *a*, *b* ; *c*, of the Dog.

work was not accessible to me, yet I do not doubt but that these cells were the same as those, which I succeeded in getting a representation of, taken from the Steer and the Dog after treating the testicle with chromic acid at ¼ per cent. strength or iodized serum (for 24 hours).

Merkel ‡ also discovered these cells, and believes them to constitute an open cellular network, symmetrically permeating the entire seminal tubule, like a sponge, without any fibrillar offshoots, but anastomosing by flat processes from the cells.

The significance of these cells is at present date unknown.

The contents of the seminal tubules, as Henle has correctly stated, are often found arranged in a radiated manner. Within the outside zone of

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* *Handbuch der Eingeweidelehre*, S. 358. † *Handbuch der Gewebelehre*, S. 530.
‡ *Göttinger Nachrichten*, 1863, Nr. 1, S. 7.

cells, which has just been described, are found others, differing from them, as well as from each other, but which have the same ultimate destiny, and therefore may be called at once seminal cells. Two typical forms of these cells

Fig. 193.

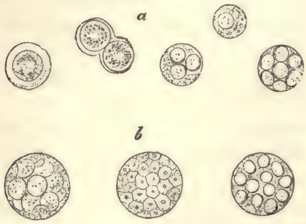

Fig. 193. Seminal cells of the Dog and Steer. *a*, cells from the seminal tubules of the Dog with one, and others with many nuclei; *b*, multi-nucleated cells from the Steer.

Fig. 194.

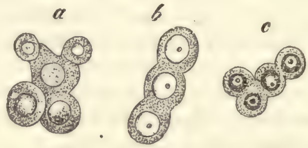

Fig. 194. Budding cells and chains of cells from the Chaffinch, *a*; Goldfinch, *b*; and brown Land-frog, *c*.

may be observed, the one with dark granular nuclei, and the other with bright nuclei, with or without nucleoli. The number of the nuclei is very variable. Cells with one and two nuclei are most numerous, but the number of nuclei may reach thirty or more.

Many forms indicate an energetic cell proliferation. Budding cells may be seen, and chains of cells very similar to Pflüger's * " Egg-chains " (Eiketten).

In Invertebrates the cell proliferation very commonly takes place by sprouting or budding. In this way the mulberry-like clusters of cells are formed, which are seen in the testicles of many of the lower animals. Constriction of the nucleus, as it takes place before segmentation, may be very beautifully observed, especially in young animals.

Fig. 195.

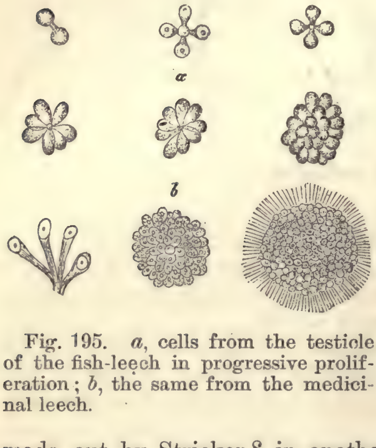

Fig. 195. *a*, cells from the testicle of the fish-leech in progressive proliferation; *b*, the same from the medicinal leech.

Both the singly-nucleated and the many-nucleated seminal cells manifest, besides these indications of proliferation, still another expression of their life, by their amœboid movements, which were first noticed by me,† and since then have been discovered in all classes of animals. In the brown Land-frog, as well as in the Vine-snail, I have observed little non-nucleated masses, apparently of unconsumed protoplasm, undergoing very active changes of form, an occurrence which has been described in a similar manner by Grohe,‡ and made out by Stricker § in another region, namely, in the milk of lying-in women.

* *Ueber die Eierstöcke der Säugethiere und des Menschen*, S. 53.
† *Ueber eine neue Art amœboider Zellen*, Schultze's *Archiv*, 1, S. 68.
‡ Virchow's *Archiv*, Bd. xxxii., S. 416.
§ *Wiener Sitzungsberichte*, 1866, S. 184.

The Vasa efferentia possess a simple cylindrical epithelium with short cilia. In the canal of the epididymis the epithelium is composed of cells with very long oval nuclei supplied with long tufts of cilia. Under this layer comes a second of small round cells with circular nuclei. O. Becker found also ciliated cells in the Hydatids of Morgagni—as I am able to certify.

Fig. 196.

Fig. 196. Cells, *a*, and nucleus, *b*, from the testicle of the brown Land-frog.

Fig. 197.

Fig. 197. Amœboid bodies from the testicle of the Rana temporaria.

The Various Forms of Seminal Elements.—Besides the cellular elements, which fill up the tubules of the testicle and have just been described, we find other figures of characteristic shape in adult animals, chiefly in the centre of those parts of the gland whose function is to produce semen. These are the seminal elements, which were first discovered by John Ham of Arnheim * in Human semen after it had been voided. They have since been thoroughly studied and have been named Spermatozoa, Spermatozoids, Spermatoids, or Zoospermata.

They supply the male procreative factor and are constant in the species, but vary greatly in form in the different classes of animals.

Protozoa.—Seminal elements have been already found in all the divisions of the animal kingdom. Even the Infusoria possess them. Here they were first described by John Müller in the Paramecium aurelia, as thread-like bodies, which fill up the enlarged nucleus. Subsequently they were further investigated by Claparède, Lachmann, Lieberkühn, Balbiani, and Stein.

In the Sponges (Spongilla) Lieberkühn discovered Zoospermatic corpuscles composed of an oval head and a tail.

Cœlenterata.—The seminal elements of the Cœlenterata display a round or oblong head with a tail attached: Actinia, Hydra, Chrysaora, Eudoxia, Rhizostoma, Athorybia.—(v. Siebold, Kölliker, Heine, Busch, Gegenbaur.)

Echinodermata.—We find a similar form in the rounded bodies and fine hair-like tails of the Echinodermata. Holothuria, Spatangus, Echinus, Asteracanthion.—(Valentin, Peters, Kölliker.)

Worms.—Worms show a great variety in the forms of their seminal elements. While the Cestoidea and Trematoda (v. Siebold, Kölliker) as well as the Turbellaria (Max Schultze) possess hair-like seminal elements, we find in the Nematoidea very peculiar shapes, with club-like or staff-like forms (Reichert, Schneider, Meissner, Claparède). Schneider discovered amœboid movements in these elements. The Sternaspis, according to Max Müller, possesses short seminal elements running to a point at one end. Rain-worms have seminal threads a little thickened at one end. In the Branchiobdella they appear very thin and drawn together at one end into a spiral form —(v. Siebold.)

In the Thread-worms the seminal elements have been found to possess globular or nearly pyriform heads and fine tails: Phyllodoce, Syllis—(Ehlers, Keferstein.)

Arthropoda.—The seminal elements of the Arthropoda are especially

* Halbertsma, *Archiv für die holl. Beiträge*, 1866, S. 232.

interesting from their greatly varied structure. Thus Leydig describes in the Notomata Sieboldii elements curved into a crescentic shape, with nucleus and nucleolus, having a distinct undulating membrane attached to one border. Others are like a stout little rod, swelling out in the middle. Here then two forms of seminal elements are found in the same individual.

The Cirripedia possess also simple hair-like seminal elements: Balanus, Lepas (v. Siebold, Kölliker). Frey and Leuckart represent the seminal elements of the Caligus as oval bodies which have the genetic significance of nuclei. In the Cyclops quadriformis, according to Zenker, they are staff-like and wound around twice. In the Cyclopsina, according to v. Siebold, they have an oval form.

The seminal elements of the Ostracoda possess a very wonderful and complicated form, according to the representations of Zenker and Metschnikow. In the Cypris ovum they are three times as long as the entire animal and have the form of a spiral rod, bordered along its side by a flat spiral. The seminal elements of the Cythera viridis present also a very unsymmetrical figure. According to Zenker they are possessed of a whip-like appendage. They are broad and sharply cut at one end, while the other end is pointed and has a process attached to it at a right angle which appears twisted like a band around its axis. The Argulus has seminal threads, according to the observations of Leydig, while the seminal elements of the Phyllopoda (Artemia, Branchipus) were observed by him to retain the cellular form. They are small vesicle-like bodies about 3μ in diameter, containing a bright speck. Leydig represents the seminal elements in most of the varieties of the Daphnida as small, rod-like forms. In some varieties he observed cells possessing bodies like nuclei with long and stiff outstanding rays (Daphnia rectirostris). The species Polyphemus is furnished with cells with uncommonly large rays.

In this animal as well as in other Daphnida Leydig saw cells displaying amœboid movements.

We are made acquainted with the very peculiar seminal elements of the Decapoda by Henle, v. Siebold, Kölliker, Frey, and Leuckart.

They are stout little cell-like figures with thread-like processes radiating from them. Owsjannikow makes the important announcement that these rays can be drawn in again, whereby the seminal element assumes a perfectly round shape.

The seminal elements of the Mysis are filamentous (v. Siebold, Frey, and Leuckart).

In the Crangon and Palæmon, according to the investigations of v. Siebold, they have the appearance of little flattened vesicles from the midst of which a sharp point projects.

In the Amphipoda and Isopoda we find stiff threads either running to a point at both ends (Oniscus) or having at one end a cylindrical pointed appendage (Asellus). In this Asellus the upper portion of the thread is bent at an angle and breaks off easily near its head, a circumstance which has given rise to a description of two forms of seminal elements in these Isopoda (Zenker).

In the Arachnida a wide difference in the form of the seminal elements is noticeable in the different orders. They are simple hair-like forms, in the Scorpio europ., exhibiting lively movements according to Kölliker. Those of the Tardigrada are spindle-shaped, with an oval head which continues into two terminal vibrating tails (Doyère, Greiff).

In the Araneides we find corpuscles devoid of motion, of rounded or kidney shape, with round or oval nuclei: Tegenaria, Lycosa (v. Siebold).

The Acarides show globular, spindle-, or club-shaped, or staff-like seminal elements: Trombidium, Bdella, Hydrachna, Ixodes (v. Siebold). Among the contents of the testicle of the Atax, Claparède saw cell-shaped seminal elements, spherical corpuscles with little rod-like nuclei.

The seminal elements of the Miriapoda offer two different types. Those of the Chilognatha are spindle-shaped or conical stiff figures: Glomeris, Julus (Leuckart). The Chilopoda on the contrary possess long threads, endowed with motion: Lithobius, Geophilus (Stein).

The class of Insects present almost universally hair-like seminal elements pointed at both ends. Their motion is wave-like, serpentine often, with one end stiff. In dilute fluids they often draw themselves into the shape of a scoop.

Fig. 198.

Fig. 198. Seminal elements of the Blaps mortisago.

Fig. 199.

Fig. 199. Seminal elements of the Helix nemoralis.

A deviation from this simple form has been recognized only (by v. Siebold) in the Locusta and the Decticus. These Grasshoppers possess a seminal element which is long drawn out and has an angular appendage attached to one end of it.

Mollusca.—The seminal elements of the Bryozoa are pin-shaped, with the head more or less flattened: Alcyonella (van Beneden, Dumortier). In the Flustra carnosa they are linear—bent in a slightly undulating manner. In the Alcyonidium gelatinosum the head is pointed, has one surface arched and the other smooth, and a tail attached which becomes thicker at its middle (Kölliker).

In the Salpa we find the hair-like form again, while in the Ascidians they were observed (Kölliker) with a cylindrical, pyriform, or elliptical head to which a hair-like tail was attached: Cyclas, Unio, Anodanta, etc. (Wagner, v. Siebold).

The seminal elements of the Cephalophora show a great diversity of form. In the Pteropoda they are described by Gegenbauer as thickened and slightly drawn into a spiral at one end, while the other end runs off into a fine thread, which swells out into a little vesicle before it terminates.

In the order of the Gasteropoda also we find much diversity in the form of the seminal elements. Some have oval or pyriform heads, sometimes showing a central contraction: Chiton, Trochus, Patella, Haliotis (Kölliker, Wagner, Erdl); others are hair-like, pointed at both ends: Turbo, Buccinium, Purpura. In the Doris there is a little thickening near the end and they appear to be slightly twisted (Kölliker). Sometimes they have a little pointed knob at one end; Lymnœus, Planorbis, Helix (v. Siebold, v. la Valette St. George).

Particularly wonderful is the occurrence of two forms of seminal bodies in the Paludina vivipara, discovered by v. Siebold and afterwards very ex-

haustively described by Leydig. Short seminal threads are seen twisted at one end like a corkscrew and near by other larger bodies of rod-like form, from the thicker end of which springs a tuft of short hairs.

Fig. 200.

Fig. 200. The two forms of seminal elements of the Paludina vivipara.

The seminal elements of the Heteropoda consist of a longish body, rather thicker in front, drawn out posteriorly into a tail which becomes finer and finer toward the end: Atlanta Carinaria (Milne-Edwards, Gegenbauer).

In the Cephalopoda we find cylindrical heads with their hair-like tails: Loligo, Sepia, Sepiola (v. Siebold, Milne-Edwards, Peters), or simple hair-like forms: Octopus (Philippi).

Fishes. — The seminal elements of the Amphioxus are filamentous, according to Kölliker, with rounded heads, which are rod-like or egg-shaped in the Lamprey: Petromyzon fluviata, marinus (Ecker, J. Müller). The Osseous Fishes commonly possess very small pin-like seminal elements: Perca, Cyprinus (Wagner, Kölliker), which in the Cobitis are provided with a little knob below the head (Wagner, Ecker). In the Salmona the head is oval, pointed in front and having a form like the heart on playing cards. This head is formed of two parts separated by a shallow furrow (Owsjannikow).

Fig. 201.

Fig. 201. Seminal element of a Canary-bird.

The seminal elements of the Dog-fish and Roach are by far larger, and have spindle-shaped heads often spirally twisted: Squalus, Torpedo, Raja (Wagner, Ecker, v. la Valette St. George).

Amphibia.—The seminal elements of the Triton and the Salamander afford very striking figures, and on that account have been the subject of exhaustive investigations (v. Siebold, Czermak). The spindle-shaped head is continued into a long tail, along the long axis of which is attached an undulating border like a shirt-frill.

In the Pelobates the head is very long and twisted into a spiral (Wagner, Leuckart).

The seminal elements of the Bombinator are spindle-shaped. A thin undulating border skirts along the side as in the case of the Salamander (Wagner, Leuckart, v. Siebold).

In the Frogs of this region, Rana esculenta and temporaria, the seminal elements differ, in that those of the former have a cylindrical head-end, while in the latter it appears nearly linear.

Reptilia.—The seminal elements of the scaly Amphibia have cylindrical or spindle-shaped heads with long tails: Lacerta, Coluber (Ecker).

Birds.—We find again a similar form in Birds. The head is either simple, cylindrical, straight, as in the Dove, Heron, Sea-gull, Birds of prey, and Ox-eye-creepers, or drawn to a point at both ends and with a corkscrew-twist: Singing birds (Wagner, Leuckart, v. la Valette St. George).

Mammalia.—The seminal elements of Mammals are constructed according

to a common type in so far as this, that they consist of a thickened, more or less orbicular head with a thread-like tail attached.

Fig. 202.

Fig. 202. Seminal elements of the House-mouse.

In the Boar the head is egg-shaped, with the point turned towards the tail and equally flattened on both sides. The same obtains in the Ram, Steer, Stallion.

On the other hand the form of the head in the Rodentia is very variable.

In the Rabbit the head is oval, flattened on the side, with the point cut short at the point of junction with the tail. In the Guinea-pig it is a nearly circular disk, with a peculiar hood-like appendage at the upper border.

In Rats and Mice the head looks something like a hatchet-head, and the tail attached like the handle of the hatchet. The upper end of the head is bent back, long and pointed in the Rat, shorter in the House-mouse, and curved in the Field-mouse.

In the Dog the head is pyriform, in the Cat egg-shaped: the tails spring from the broader ends.

In the Hedgehog the head is, as it were, cut off toward the lower end. The tail is inserted at the side.

In the Bat the head is also cut off at one end, but the tail is inserted into the centre of the under border.

In Monkeys the head is egg-shaped, with the broad end turned toward the tail. The seminal elements of Men have an oval head, whose lower border, turned towards the tail, is thicker and rounded off. The head continues forward into a thin hood somewhat deepened centrally. On this account the head, seen from the side, appears more or less pyriform. Leuckart called my attention to the fact that this thickening is rather more prominent on one surface than the other. The length of the head is 5 μ, the breadth 3 μ, the greatest thickness 1 μ. The tail is a little reduced at its attachment to the head, then gets thicker (to 1 μ), and continues (to a length of 50 μ) to a very fine point.

Fig. 203.

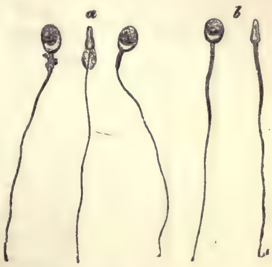

Fig. 203. Seminal elements of Man; *a*, undeveloped; *b*, mature.

Structure of the Seminal Elements.—We have received recently some interesting communications concerning the more minute structure of the seminal elements of the Vertebrates.

According to Valentin * the spermatoid elements of Bears contain three rounded striped bands, a forward, a middle, and a posterior band. Hartnack considers these bands to be elevations and depressions, which disclose themselves by a change in the light and shade, according to the direction in which the figure is illuminated. Valentin and Thury give plates of these bands in the seminal elements of Bears, Rabbits, and Dogs. The Cat, Ram, and Guinea-pig also show them, but less distinctly. With powerful lenses they can be seen without difficulty as I have drawn them,† from the Dog

* *Zeitschrift f. r. med.* 3 R., Bd. 18, S. 217, u. Bd. 21, S. 39.

† *Ueber die Genese der Samenkörper*, M. Schultze's *Archiv*, 1867, Bd. iii. Taf. xiv., Fig. ii. and v.

and Rabbit, with a No. IX. Hartnack lens. They may be recommended as test objects.

Grohe,* after very exhaustive investigations, concludes, that the seminal elements consist of two different parts, a structureless envelope and a contractile content, which is present in greatest abundance in the head. The bands, above described, he attributes to a difference in the distribution of the contents within the envelope.

He is sustained by Schweigger-Seidel † in so far as the latter assumes an outer containing sheath, and a contained mass, although he only succeeded in demonstrating the former as a distinct envelope in Amphibia and Birds.

Between the head and the tail Schweigger-Seidel distinguishes a so-called "Middle-piece," which he establishes in the Frog, Triton, Cock-finch, and many Mammals. I have already been able to confirm his statements in Man, Hedgehog, Dog, Guinea-pig, Rabbit, Frog, and Triton,‡ as has also Kölliker. §

In apparently mature seminal elements I did not always succeed in making out that boundary of the Middle-piece which lies towards the tail, consequently I was obliged to resort to an investigation of semen taken from within the female genital passages. A female Bat, which had been sitting in solitude for 36 hours, gave me the desired opportunity. I found the vagina and uterus filled with seminal elements in active motion. All exhibited a very marked Middle-piece. The length of the Middle-piece ranges according to Schweigger-Seidel between 9 and 23 μ. In Man it reaches 6 μ.

Fig. 204.

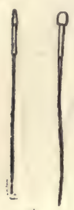

Fig. 204. Seminal elements of the Bat, with distinct Middle-piece.

The Motion of the Seminal Elements.—In certain animals, as I have already remarked, the seminal elements are entirely motionless even within the female genital passages: Oniscus; in others we find the commencement of motion in the amœboid changes of form: Nematoda (Schneider), Daphnia (Leydig), Crabs (Owsjannikow). The majority of seminal elements, however, are very decidedly capable of change of position. This is very much assisted by the above described undulating membranes. The motion may be uniformly progressive (in a forward direction), as, for example, in the Canary-bird, in which case the entire seminal body revolves with great rapidity around its own axis—or spasmodic and irregular, as in Mammals. Between these points are found all possible variations. The head-end, where it is distinguishable, goes forwards. Grohe maintains that the motion is brought about by a contraction of the contents of the head, which, however, I (with Schweigger-Seidel and Kölliker) do not admit. I have never observed that sort of change in the head, but on the other hand have often seen headless threads in most active motion. I must also dispute the assertion of Schweigger-Seidel that the Middle-piece remains rigid and takes no part in the motion.

The duration of the movements is very different, according to the medium in which the seminal elements are placed. It continues for 48 hours in the body of the animal. In the female genital passages it is still demonstrable after 8 days.

Alkaline solutions are favorable to the continuance of this motion, acid or too dilute fluids are unfavorable. Kölliker ‖ has discovered that a con-

* Virchow's *Archiv*, Bd. xxxii., S. 416. † Schultze's *Archiv*, Bd. i., S. 309.
‡ Loco citato, p. 264. § *Handbuch der Gewebelehre*, 1867, S. 530.
‖ *Zeitschrift für wiss. Zoologie*, Bd. vii., S. 201.

centrated solution of salt, sugar, or albumen will restore to seminal elements the motion which has been lost by their having been placed in water. Caustic potash and lime ($\frac{1}{32}$–50 per cent. strong) act as excitants of motion, as does also Curara in an exquisite manner. Cocaine, like sulphate of morphia, has no action upon the motion (Wagner, Kölliker, Leuckart, Montegazza). According to the latter author * the seminal elements of Man retain their power of motion from —15° to +47° C.

Frozen semen recovers its activity after thawing. It has been kept by Montegazza at 0° C. for four days without injury. Semen dried in a solution of salt or in indifferent substances can, in certain cases, according to Kölliker, be again rendered active by dilution with the same fluid or with water.

Development of the Seminal Elements.—The origin of the seminal elements has been inquired into to such an extent, that it is astonishing that the theme has not long since been exhausted. The reasons for this are to be found in the peculiar obstacles to observation offered by the minuteness of the object, the difficulty of discovering fluids (in which to carry on the observations) which will not act upon the object, and the circumstance that, at least in the higher animals, the different forms of the seminal elements, in their different stages of development, are not widely separated. Before their origin was known, as was natural, the most varied opinions were entertained concerning their nature and significance, opinions which it was reserved for after-time to overthrow.

Kölliker † first established, that the seminal elements were to be considered, not as individual living beings, but, on the contrary, as elementary portions of the organism. He taught their origin from cells, that they were formed in the cell nuclei, in which they continued for a certain length of time, and then remained rolled up in the cell, until the latter burst and they became free.

Kölliker's theory was actively opposed by Reichert, ‡ who, supported by his investigations upon the Strongylus auricularis and Ascaris acuminata, upheld that the seminal bodies, originating in elementary nucleated cells, were evolved, with all their constituent parts, by the process of cell-formation, from portions of the contents of the mother-cells.

Leuckart expresses himself as follows on the development of the seminal bodies. Sometimes, he remarks, the entire seminal cell is changed with all its parts into the seminal element, sometimes the seminal element is developed entirely from the nucleus, and finally it is sometimes formed from the contents of the seminal cell. In the last case Leuckart does not consider the developmental vesicles of the seminal cells as nuclei, but, on the contrary (like Kölliker), as cells formed endogenously. Later researches into the subject led Kölliker to withdraw his former opinion. §

He concluded that the seminal elements were formed not within the nucleus but by an outgrowth of the same in length—nevertheless this process was well pronounced only in the case of Mammals. The true seminal cells are especially the smaller cells and the large cysts with many nuclei. The nuclei of these cells and cysts become lengthened and flattened. Then the nucleus separates itself into a forward part, with a dark contour and a posterior smaller portion with pale borders. While at the forward pole a very

* *Journal de l'anatomie et de la physiologie*, 1868, S. 184.

† *Beiträge zur Kenntniss der Geschlechtsverhältnisse und der Samenflüssigkeit wirbelloser Thiere*, 1841; *Die Bildung der Samenfäden in Bläschen.*

‡ *Handwörterbuch der Physiologie* v. Wagner. Bd. i., S. 851.

§ *Zeitschrift für wiss. Zoologie*, Bd. viii., S. 201.

small knobbed thickening frequently shows itself, there proceeds from the posterior end a shorter, thread-like appendage, which soon becomes a longer thread, while at the same time the paler, posterior part of the nucleus increases steadily in size. The mature seminal elements lie for a certain time rolled together in their mother-cell and become, for the most part, so free that they break through the mother-cell, the head at one side and the tail at the other. The remains of the mother-cell continue, for a certain time longer, still attached to the seminal elements, partly as a hood-like covering for the head, but especially as appendages to the tails. Finally, Kölliker resumes his theory of the development of the seminal elements in the entire animal kingdom as follows:—

1. The fructifying elements of all animals are developed by a direct transformation of the nuclei of the seminal cells.

2. The seminal elements, devoid of motion, found in the Arachnida, Myriapoda, etc., are simply altered nuclei or nuclei changed in form.

3. In the case of the seminal elements endowed with motion, or the seminal filament, a movable tail has been developed out of the nucleus near the head.

Ankermann * believes the seminal elements of the Frog to be formed, each one for itself, out of a nucleated cell. The nucleus grows into a head, while the tail, he believes, is formed by a drawing out of the cell membrane.

Pflüger † describes the seminal element as a small ciliated cell and attributes its origin to a free cell-formation.

Henle ‡ assumes with Kölliker, that in Man and in Mammals the head of the seminal element is a metamorphosed nucleus, and considers its permanent connection with the cell as indispensable for the formation of the tail.

Grohe § believes it probable that the contractile substance of the seminal element is formed independently from the cell contents, like the sarcous element in muscular cells.

According to the investigations of Schweigger-Seidel the seminal element is not simply a modified nucleus, but corresponds to an entire cell, as a metamorphosed singly-ciliated cell.

In my ‖ first communication, which appeared at the same time, I expressed it as my conviction, that a share in the formation of the seminal element must be ascribed to the protoplasm of the seminal cell as well as to the nucleus, and endeavored to give a representation of the development of the seminal elements in Mammals, Birds and Amphibia. In a second communication I was able to add my investigations made upon the Arthropoda and Mollusca.

Like Zenker in the Asellus¶ and Keferstein ** in the Helix pomatia I observed a development of seminal elements with persistence of the original nucleus.

Since then Kölliker †† has again given his views on the development of the seminal elements, but he finds no occasion to withdraw from the ground he assumed previously.

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* *Zeitschrift für wiss. Zoologie*, Bd viii., S. 129.
† *Ueber die Eierstöcke*, S. 93.
‡ *Handbuch der Eingeweidelehre*, S. 356.
§ *Loco citato*, p. 426.
‖ Max Schultze's *Archiv*, Bd. i., S. 403.
¶ *Archiv fur N.*, S. 20, 103.
** *Die Klassen und Ordnungen des Thierreiches*, Bd. iii., S. 1215.
†† *Handbuch der Gewebelehre*, S. 530.

Owsjannikow * gives us very interesting data concerning the development of the seminal elements in Fishes, which had been but little studied before him. The testicles of the Salmon contain epithelial cells chiefly of a cylindrical form and lying in two rows. The cells have a large white nucleus with distinct nucleoli, and a protoplasm. The cells of the second and third rows show segmentations of the nucleus and protoplasm. The cell thus increases greatly in size and may contain from 10 to 15, and more, young cells, without losing its form. The nucleus of the cell supplies the head and the surrounding protoplasm the tail.

Metschnikow † has contributed some important facts concerning the development of the seminal elements, which, unfortunately, were not accessible to me. According to a very full reference by Hensen and Kupffer he discovered seminal cells with granular nucleus in Rain-worms. The granules collect together within the nucleus and form a smooth ball, which becomes lengthened out with the nucleus, while the plasma of the cell grows out on one side into a tail.

In the river Craw-fish, he states that the head is formed out of an independent intercellular structure, which lies near the nucleus.

Also in the Fly the nucleus has no rôle to play (according to Metschnikow), but the granular mass, out of which the seminal element is formed, becomes divided up, and afterwards melts down again into a simple element. In the same manner the large seminal elements of the Cyprois are formed near the nucleus.

Balbiani ‡ also observed a body near the nucleus, which became developed into the head of the seminal element.

I have published my own investigations to date on the development of the seminal elements, and will now briefly express my views on the sub-

Fig. 205.

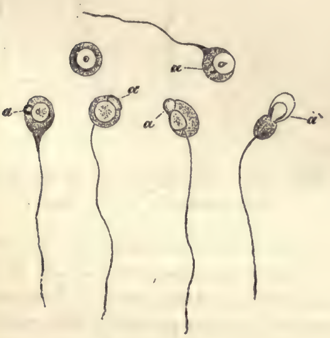

Fig. 205. Development of the seminal elements of the Guinea-pig. *a*, hood-like appendage.

Fig. 206.

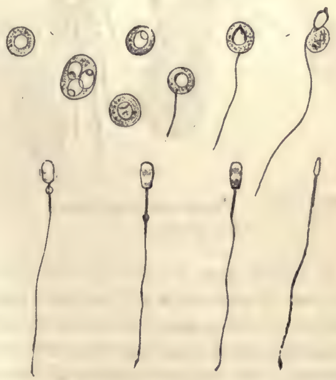

Fig. 206. Development of the seminal elements of the Dog.

ject. I have already stated at length the manner of proliferation of the seminal cells. I regard singly- or many-nucleated cells, whose nuclei appear granular, as the point of origin in the development of the seminal elements.

* *Bulletin de l'Académie de St Pétersbourg*, T. xiii. p. 245.
† *Mémoires de l'Académie de St. Petersbourg*, 1868.
‡ *Journal de l'Anatomie et de la Physiologie*, 1868, S. 218.

Next the nucleus becomes clear and shows a peculiar change. In the Guinea-pig it retains for some time a round mucleolus, while in its upper half an accumulation occurs in the shape of a little knot, which, when seen with the nucleus by a side view (on section as it were) appears like a seal-ring. The nucleus becomes lengthened out as the next step, and projects out from the cell on one side. The nucleolus has now disappeared. At the other side of the cell the tail sprouts out from the protoplasm and becomes attached to the nucleus. The cell substance, which in the beginning surrounded the nucleus and the upper part of the tail, like a sack, disappears more and more and finally attaches itself—since the head has become free at one side and the tail has grown out from the other—attaches itself finally, I say, as a larger or smaller appendage to that section of the tail which corresponds to Schweigger-Seidel's "Middle-piece." This forms, to a certain extent, the point of junction between the head and the tail. The little knob on the nucleus has now become transformed into the hood-like appendage.

In the Dog I have noticed two peculiar changes in the nucleus; the one, that a little vesicular body shows itself at one side of the nucleus; the other, that the upper half of the nucleus possesses a thicker contour than the lower half.

Whether the seminal cell have one nucleus or many is of no importance, since the many-nucleated cell is to be considered only as the sum of several cells, whose number is represented by the number of nuclei, together with a certain amount of cell-substance surrounding the nuclei.

Fig. 207.

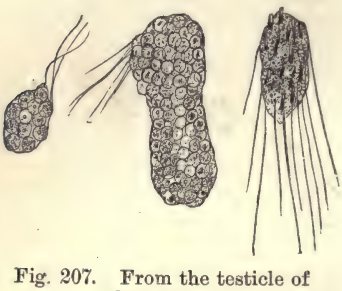

Fig. 207. From the testicle of the Mouse.

Fig. 208.

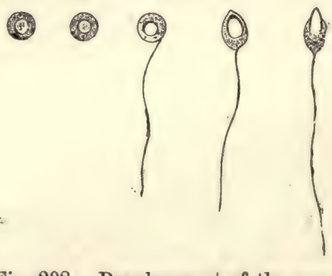

Fig. 208. Development of the seminal elements of the Mole.

Kölliker says "that the seminal cells have no essential share in the formation of the tails of the spermatozoa; the most that can be said of it is, that very often many seminal elements are formed in a single cell." Properly speaking, each seminal filament is formed out of its own peculiar cell, yet in this case the cell-substance of the individual cells is not isolated.

Thus Kölliker still assumes the formation of the tail from the nucleus.

I must remark that I have never seen nuclei with stump-like tails without cell-substance, nor do I any longer find tails rolled up together, since the proper degree of concentration of the fluid to be employed in studying them has been known to me.

Kölliker believes that the nucleus, in its development for the formation of the tail, first grows out at one pole into a slender tube. I have seen this appendage to the nucleus in the seminal elements of the Steer in a solution of common salt, ½ per cent. strong, and frequently in a solution of chromate of potash. I consider them with Henle as remains of the seminal cells.

The development of the seminal elements of the brown Land-frog had, hitherto, to be considered as very wonderful and as exceptional among the Vertebrates. After Remak, Ankermann, and Kölliker had already studied them, they were investigated anew by Neumann. It would lead me too

Fig. 209.

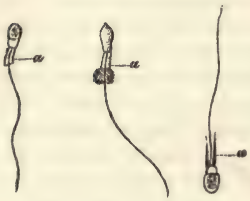

Fig. 210.

Fig. 209. Seminal elements from the Steer, with appendage from the nucleus.

Fig. 210. Development of the seminal elements of the Rana temporaria.

far to repeat here all the opinions which have hitherto been advanced upon the subject. I will briefly detail my own investigations. The seminal elements of the Rana temporaria are developed exactly like those of the Rana esculenta. Their seminal cells form balls, like those found in the testicles of

Fig. 211.

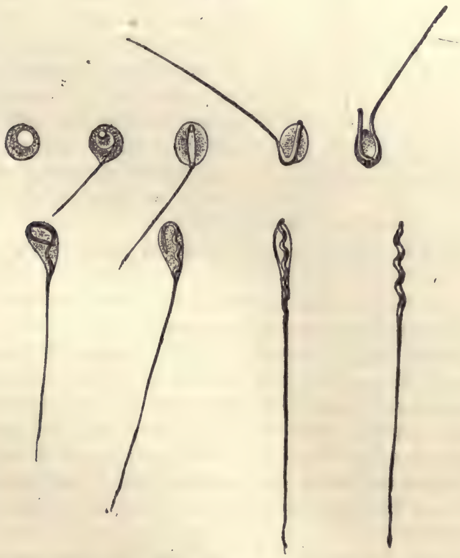

Fig. 211. Development of the seminal elements of the Raja batis.

Insects. These balls are surrounded by a delicate membrane, which contains some large scattered nuclei, each with a nucleolus. The cells, at first large and few in number, with granular nuclei, increase by segmentation to a con-

siderable cluster. Each one of the cluster produces a seminal element, the nucleus becoming brighter and growing into a head, the cell-substance into a tail. Finally the membrane surrounding the cluster bursts and discloses, besides the remains of the protoplasma, several nuclei, which, however, never had anything to do with the seminal cells. To study the development of the semen in Fishes I found a very suitable object in the testicle of the smooth Ray. The seminal elements seemed to be formed from large cells (10 μ) with bright nuclei (5 μ). As in some Mammals, I noticed at one side of the nucleus a little vesicular excavation. Then the nucleus increased in length and something like a little knob appeared at its upper end. From the opposite side of the cell the tail sprouted out and soon became joined to the nucleus. The head constantly increased in length and appeared bent, being still surrounded by the cell. Then it began to become twisted upon itself like a corkscrew. Finally it straightened itself again and appeared as a regularly formed spiral, 34 μ long, with a straight tail 85 μ long.

Fig. 212.

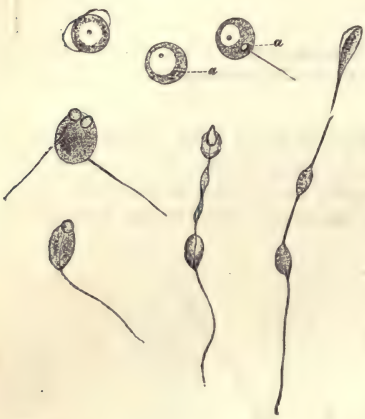

Fig. 212. Development of the seminal elements of the Helix nemoralis.

Thus we see, that a perfect similarity in the development of the seminal elements obtains for the Vertebrates. For the Invertebrates my investigations are not exhaustive; but this much is certain, that, in the Mollusca and the Arthropoda, a portion of the tail is formed from a shining body lying near the nucleus. Whether this body is a product of the nucleus, remains doubtful. I have often seen it double, with several nuclei lying near it—and again, often, there is only one nucleus-like mass out of which it appears to proceed. That upper portion of the tail, so formed, always appears thickened at first, although no real body is distinguishable (to mark its place) in the mature seminal element.

Here also the tail seems to sprout out from the protoplasma.

Vessels and Nerves of the Testicle.—The blood-vessels of the testicle, which are derived from the internal spermatic artery, enter the gland at its posterior border and ramify partly in the Corpus Highmori, and partly upon the surface of the organ, underneath and within the substance of the Albuginea. From both sides they permeate the parenchyma of the gland and surround the seminal tubules with a capillary plexus of wide meshes. From these vessels the distribution to the Epididymis is rather scanty, since the deferential artery assists in the vascular supply of this part. The veins comport themselves like the arteries and come out at the posterior part of the Albuginea ascendens.

The course of the lymphatics in the testicle has been made out very thoroughly of late by the investigations of Ludwig and Tomsa.* That the lymphatics reached a considerable development in the testicle was already

* *Wiener Sitzungsberichte*, Bd. xliv., S. 221.

known since Panizza's * investigations, but their origin had been hitherto undetermined.

Ludwig and Tomsa have now proved that the lymphatic vessels of the gland take their origin in wide canals without special walls, which run between the seminal tubules. His † confirmed this statement and succeeded (by means of a solution of silver) in demonstrating, that the roots of the lymphatics in the testicle are lined by a characteristic epithelium. Frey ‡ also sustains the views of these investigators, basing his opinion upon numerous injections. Tommasi § treated fresh sections of testicle with a silver solution, 4 per cent. strong, and came to the conclusion that the lymphatic vessels of the testicle end in a true system of lacunæ in which the seminal tubules are suspended, and further, that the walls of these lacunæ are covered by an epithelium, like that of the lymphatic vessels, which is also continued upon the seminal tubules.

Kölliker ‖ corroborates these views. He found in the Steer, that the diameter of the finest tubes was 40–90 μ, while the epithelial cells were 90–110 μ long and 10–20 μ broad. He also succeeded (as indeed I did very easily) in demonstrating the epithelium on the seminal tubules by treatment with nitrate of silver.

Concerning the nerves coming from the internal spermatic plexus, until very recently, no investigator has succeeded in tracing them further than the plexus.

Lately, Letzerich ¶ has described the manner of termination of the nerves in the testicle of Mammals and of Man.

In fresh seminal canals, or in such as had remained 24 hours in a solution of chromic acid, at $\frac{1}{20}$–$\frac{1}{25}$ per cent. strength, Letzerich saw fine nerve fibres penetrating the connective-tissue layer and the Membrana propria, and ending between this layer and the first row of cells in darkly granular masses. They sank into an irregularly formed, shining, granular mass of protoplasm, and terminated in it in a head, which was faintly brilliant in fresh preparations but more glittering in preparations which had been slightly hardened. The nerve-sheath did not penetrate the mass of protoplasm, but appeared to terminate in an uncommonly fine membrane which surrounded the latter, so that the real ends of the nerve-fibres were formed of the axis-cylinders, comparatively short and broad, and provided with a round and shining knob, which was usually attached excentrically.

These observations, which, if accurate, are especially important, have not yet been confirmed. I myself have thus far vainly endeavored to see the appearances above described.

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* *Osservazioni*, Pavia, 1836, Tab. viii.

† *Zeitschrift für wiss. Zoologie*, S. 469.

‡ Virchow's *Archiv*, Bd. xxviii., S. 370.

§ Virchow's *Archiv*, Bd. xxxviii., S. 370.

‖ *Handbuch der Gewebelehre*, S. 533.

¶ Virchow's *Archiv*, Bd. 42, S. 510.

CHAPTER XXV.

THE OVARY AND PAROARIUM.

By W. WALDEYER.

In the animal kingdom the ovaries are coextensive with sexual reproduction. If in many instances their structure is very simple, so that they can hardly be spoken of as special organs, yet, with perhaps the single exception of the Porifera, the formation of female germs is restricted to certain groups of cells and certain portions of the body; and herein we find a contrast to the manner in which germs and buds are formed in sexless generation. In the ovaries the eggs not only receive their origin, but are also brought to their full development, are invested with special membranes for their protection, and are sometimes even retained for years. The higher we rise in the scale of organization, the more complicated, as a general rule, does the structure of the ovaries become.

In the three higher classes of Vertebrates, the Mammals, Birds, and Reptiles, and probably also in the Selachia—in reference to which, however, I myself have made no investigations—the fully developed ovary is found to consist of these essential elements: (1) the *ovarian epithelium* or *germ-epithelium;* (2) the *ovarian follicles* or *Graafian follicles*, in which (3) the *eggs* are contained. These structures are held together and supported by a stroma of connective tissue which is extremely rich in vessels, nerves, and muscular tissue.

In the first place let us familiarize ourselves with the arrangement of the above-mentioned parts as they are seen near the surface, in the fully developed ovary of a Human being or one of the larger Mammals, and in the adjoining sagittal section through the ovary of a full-grown Dog.

The ovary seems to be enveloped in a duplicature of the posterior portion of the Lig. latum, and is consequently covered by the Serosa. A careful observer will also notice that the base of the organ is encircled by a white line, indicating where the peritoneum ceases and the superficial epithelium of the ovary—the germ-epithelium—begins. The latter (see figs. 213 and 214) may be distinguished from the familiar flat-celled epithelium of the peritoneum by its cylindrical cells, which are at the same time more granular. The germ-epithelium imparts to the surface of the ovaries a dull gray appearance which contrasts distinctly with the brilliant surface of the Serosa, and looks more like that of a mucous membrane. If we wished to obtain the peritoneum as a separate membrane, we should find that it came to an abrupt termination at the ovary, in exactly the same manner as at the pavilion of the tube. The equalness of these two localities and the right to consider the superficial epithelium of the ovary as equivalent to the epithelium of a mucous membrane are justified by the simple circumstance that in many ovaries the epithelium of the tubes is continuous with that of the ovary, which only lacks the cilia of the former.

The covering of germ-epithelium is wanting in the ovaries of Amphibia. Osseous

Fishes and Cyclostomi; this peculiarity will be explained farther on. As to the Ganoids and Selachia I am not in possession of any facts at the present time.

Larger and smaller Graafian follicles may be seen either shining beneath the surface of the ovary, or rising up into transparent hemispherical vesicles which stand out more or less above the surface of the organ and are woven over with a narrow-meshed network of vessels, visible even to the naked

Fig. 213.

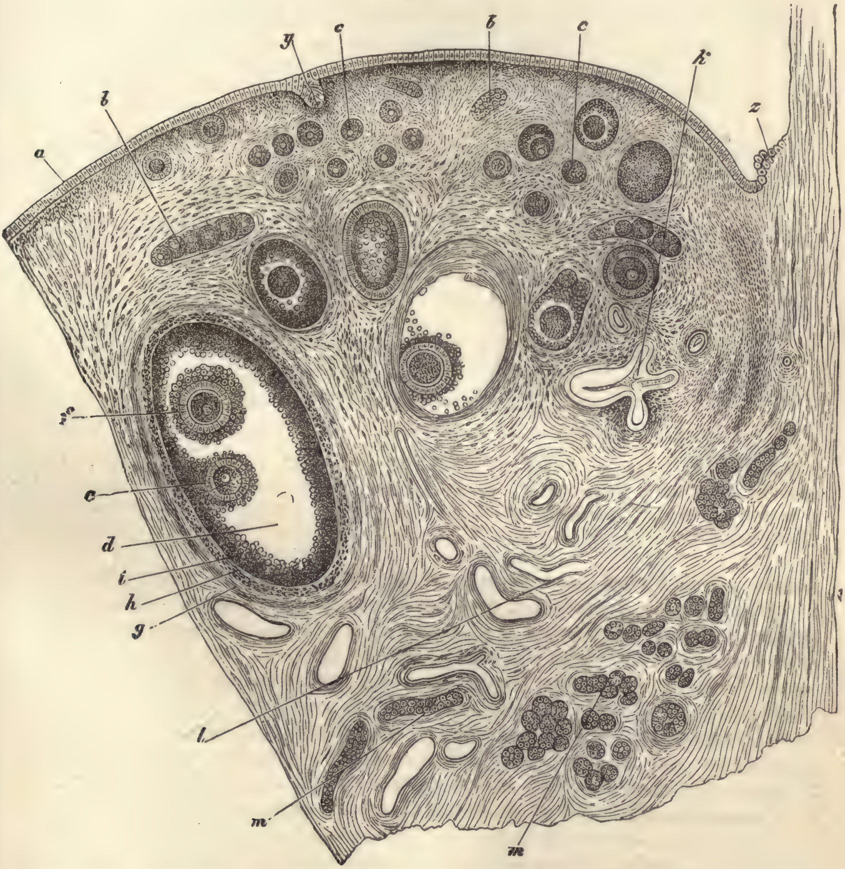

Fig. 213. From the ovarium of a rather old Bitch; portion of a sagittal section. Hartnack $\frac{3}{4}$.* *a*, germ-epithelium; *bb*, ovarial tubes; *cc*, younger follicles; *d*, older follicle; *e*, discus proligerus, with egg; *f*, epithelium of a second egg in the same follicle; *g*, tunica fibrosa folliculi; *h*, tunica propria folliculi; *i*, follicular epithelium (membrana granulosa); *k*, collapsed, degenerated follicle; *l*, vessels; *m*, *m*, cell-tubes of the paroarium: both longitudinal and transverse sections; *y*, tubular sinking in of the germ-epithelium into the substance of the ovary; *z*, commencement of the germ-epithelium close to the lower border of the ovary.

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* The numerator indicates the number of the eye-piece, the denominator that of the objective.—TRANSLATOR'S NOTE.

eye; scattered among these a few so-called "yellow bodies" may be seen—the retrograde forms of the ovarian follicles.

The perpendicular section shows us the germ-epithelium at *a*, in Fig. 213, and beneath it a layer of rather firm connective tissue consisting of several intersecting layers, in which may be seen a few ovarial tubes *b*, *b*, and some of the younger ovarian follicles *c*, *c*. Then follow the older ovarian follicles—some of which contain already nearly mature eggs—and last of all the highly vascular stroma of the hilus, which it is customary to call the *medullary substance*, in contradistinction to the above-mentioned layers, which together constitute the *cortical substance*. More appropriate would be the

Fig. 214.

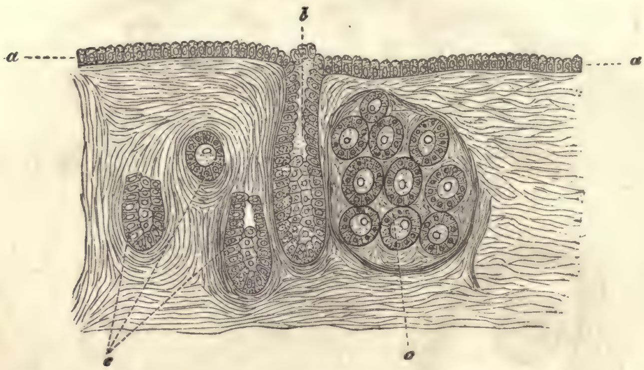

Fig. 214 (No. 14, Plate II. of my work (123)). Vertical section of the ovary of a six months old Bitch; Hartnack $\frac{2}{7}$; *a*, epithelium; *b*, ovarial tube with free opening; *c*, larger group of follicles, arranged like a cluster; *e*, oblique and transverse sections of ovarial tubes.

names *parenchymal zone*, *zona parenchymatosa*, for the cortical layer, and *vascular zone*, *zona vasculosa*, for the medullary substance. According to this scheme are constructed the ovaries of adult Mammals and Man, and, in sum and substance, those likewise of Birds, Reptiles, and Selachia. In the latter classes, especially in Birds, the ovary is subdivided in some into a few closely-packed lobules, while in others it has a clustered appearance, owing to the number and size of mature ovarian follicles, which when fully mature hang down over the surface by pedicles; this at first sight seems to establish a great difference between the usually compact form of the Mammalian ovary and the lobulated or clustered structure of that of a Bird or Reptile.

I must state expressly that this scheme only applies to the fully-developed ovary; during its development and sexual activity there is certainly no organ so changeable in form and histological structure as the ovary. Later we shall describe the various phases of its development; at present let us confine ourselves to the description of the fully-developed ovary.

In Man and Mammals the largest part of the *stroma of the ovary* is simply connective tissue. The connective tissue of the vascular zone is rather loose in texture and composed of bundles of long fibres, which are frequently woven over with elastic fibres; that of the parenchymal zone in the adult female is divided into an outer layer of compact short fibres whose bundles interlace in every conceivable direction, and an inner layer, very rich in cells, in which the follicles are situated; the large follicles extend even into the periphery of the vascular zone.

The maintenance of the existence of an Albuginea in the ovary as a separate membrane is justified at the present time more by the right of age than by the requirements of anatomy or histology. With knife and scissors no special connective-tissue membrane can be dissected off. At most there may be seen in Man under the microscope a layer of connective tissue which, as Henle (50) has correctly represented, is usually of three thicknesses, and consists of pretty short, compact fibres interspersed with a few spindle cells. The fibres of the first and third layers usually traverse the surface of the ovary in a sagittal direction, while those of the middle layer run transversely; to the whole we may give the name of Albuginea. It is to be remembered, however, that in the new-born infant and even up to the third year of life no continuous layer of fibres can be demonstrated, for the ovarian follicles and tubules lie immediately beneath the epithelium, and moreover with advancing age the number of these slightly cellular compact layers increases, so that we can sometimes find 5 or 6 of them; and finally it must be taken into consideration that the so-called Albuginea is inseparable from the underlying mass of fibres and passes imperceptibly into it.

Immediately beneath the above-mentioned parallel fibrous trabeculæ of the so-called Albuginea, follows a layer of compact connective tissue, also poor in cells, whose fibres show no special attempt at stratification, but run in every conceivable direction; toward the centre they are continuous with that layer of the stroma which is rich in cells and includes most of the follicles. All the fibres of connective tissue which are to be found in the peripheral layers appear dark like elastic fibres when cut transversely, but glossy when cut lengthwise. With acetic acid, moreover, these parts are only with difficulty rendered transparent. To render quickly visible the small follicles which are embedded here and there throughout the connective tissue, it is advisable to use caustic soda.

Deeper down the stroma of the ovary is extremely rich in cells, immediately surrounding the younger follicles. The cells are spindle-shaped and are frequently provided with long processes. Wherever the larger vascular trunks pass through this cellular layer, on their way to the surface of the ovary, large trabeculæ of connective tissue, which at the periphery spread out like an umbrella, will be found accompanying them, and may be distinguished in the midst of the more delicate cellular tissue like beams of a framework. (In regard to this point consult especially Henle (50), page 481.) In animals, and especially in those where ovulation occurs more frequently, a large number of granule-cells will be found here, showing that in this layer, where the development and retrograde metamorphosis of the follicles principally takes place, the stroma likewise undergoes manifold changes. His (52) has also demonstrated the presence in the ovary of a second variety of cells, to which he gives the name of "grain-cells," and which are in all respects like the ordinary colorless blood corpuscles. His assumption that the follicular epithelium originates from these must nevertheless be characterized as erroneous, as will be shown farther on.

The smooth muscular fibres of the ovary are restricted, at least in Mammals, to the vascular zone, which lies immediately next to the highly cellular layer of the parenchymal zone, which we have just described. They lie there in separate bundles, which follow the course of the larger and medium-sized arteries, and sometimes surround them like a sheath (see Aeby (1) and Grohe (49). They may be followed as far as to the boundary of the cortical substance, but do not enter it, however—at least in Man and the domestic Mammals; in not a single instance do they reach the wall of the follicle. The case is somewhat different in Amphibia and the Osseous Fishes, in which we find bands of smooth muscular fibres following everywhere the course of the larger trabeculæ of the stroma between the ovarian follicles, and in some instances reaching even to the outer wall of the latter. The ovaries

of the Osseous Fishes even possess a complete muscular envelope, from which numerous smaller muscular bands radiate to the several egg-bearing lamellæ.

The question concerning the relations of the smooth muscular fibres in the ovary has given rise to a controversy which yet remains unsettled; it originated more especially in the consideration whether the muscular tissue were not in some way connected with the opening of the follicles and the extrusion of the eggs. His (52), Rouget (99), Klebs (56), and Aeby (1) go the farthest in attributing to the smooth muscular tissue a large share in the composition of the ovarian stroma. His even believes that we may consider almost the whole interstitial tissue of the ovaries as a peculiarly modified and at the same time stunted muscular tissue, for which he suggests the name of "spindle tissue." The vessels of the ovary, according to His, possess no Adventitia nor Media, in the ordinary acceptation of the terms, but the fibres of their muscular coats pass on, one after another, into the stroma of the ovary; he also believes that all the spindle-shaped cells of the ovaries, are stunted muscular cells. Aeby (1) describes the smooth fibre-cells as approaching even to the outer wall of the ovarian follicles. Rouget (99) would also have the muscular bundles to stand in a peculiar physiological relation to the vessels; according to his view there exists in the ovary the same arrangement of the vessels and of the bundles of muscles, which surround them like a sheath, as is to be found in the erectile organs. While Rouget connects the mechanism of erection with the simultaneous appearance of vessels and smooth muscular fibres, he at the same time ascribes to the ovary a power of erection, which takes effect at the period of menstruation and assists in the expulsion of the egg. The peculiar connection of vessels with accompanying bundles of smooth muscular fibres in the erectile organs is a matter of fact; at the present time, however, direct observations are wanting concerning anything like an erection of the ovaries. In Frogs Pflüger (86) observed contractions of the stroma in response to direct electrical irritation, but in Rabbits he was unable to obtain any decisive results. His (52) interprets the decided bulging forwards of the cut surfaces in the fresh ovaries of the Cow as a phenomenon of contraction; Frey (40) expresses a similar view. The results of my own investigations agree best with what has been found by Kölliker (59), Henle (50), Pflüger (84) and others, according to which the smooth muscular tissue is not so extensively disseminated through the stroma of the ovary as His, Aeby, and Klebs would have us believe. Von Winiwarter (126) has recently subjected the elements of the cortical layer to an accurate histological and histochemical analysis, but was unable to prove the presence of smooth muscular fibres. Moreover, the smooth muscular fibres of the hilus of the ovary originate from bundles which radiate from the ligamentum latum into the hilus of the organ. (Consult on this point especially the statements of Grohe (49) and Luschka (72).

I have already previously spoken of the extraordinary vascularity of the stroma of the ovary; the hilus of the ovary contains a convoluted mass of broad veins which when fully injected represent a sort of vascular bulb—Rouget's (99) bulbs of the ovaries. The arteries also retain in the ovary the same winding corkscrew-shaped course which already characterizes the larger trunks—the Arteria spermatica interna and the branches of the Arteria uterina. An exceedingly rich capillary network, almost like that of the membrana Ruyschiana of the Chorioidea, will be found in the internal membrane of the follicles, which has been minutely described by His (53); it is not difficult to obtain a very beautiful view of it in a state of natural injection by spreading out the wall of a small follicle, fresh, in serum under the microscope.

According to the statements of His (52), lymph vessels are found in the hilus of the ovary; besides these there are also broad sac-like lymph spaces which surround the follicles and yellow bodies like a shell, thereby rendering their enucleation an easy matter; all these spaces can easily be injected by the "pricking method." *

No accurate information can be given at the present time concerning the

* Einstichsmethode. See Addenda.—TRANSLATOR'S NOTE.

distribution of the nerves in the ovary. In the ovaries of Rabbits, from which sections were made when in a frozen condition and then treated with the chloride of gold, I have been able recently to follow delicate nerve-fibres, which were provided with only a very thin medullary sheath, as far as between the larger follicles; their mode of termination, however, I was unable to ascertain.

The situation of the Graafian follicles in the ovary is not the same, either at the different periods of life or in the different species of Mammals; farther on, when we come to speak of the development of the ovary, we shall return to the first of these points. In reference to the few Mammals, which are frequently made use of for the purposes of investigation, it may be mentioned that in the Cat and Rabbit, a series of the smallest follicles are found gathered together in clustered groups immediately beneath the so-called Albuginea; this is Schrön's (102) "zone of cortical cells," or His' (52) "cortical zone." Schrön mistook these youngest follicles for eggs; his description of the development of the egg may therefore be accounted for by this circumstance. These clustered groups of follicles are also to be found in the Dog. (See fig. 214, *c.*) In the Cow, Pig, and Man, and as a rule in the larger animals, the follicles lie more dispersed throughout the already-mentioned highly cellular layer of the parenchymal zone,—the follicular layer,—owing to the fact that the interstitial tissue between them is more strongly developed.

In the larger Graafian follicles (see fig. 213, *a*) a wall of connective tissue may be distinguished—Von Baer's (2–5) *Theca folliculi*—in which two layers are recognizable, Henle's (50) so-called *Tunica fibrosa* (the outer layer) and the *Tunica propria folliculi.* The Tunica propria in Mammals carries on its inner surface a multiple layer of cylindrical epithelium, the *follicular epithelium* or *Membrana granulosa* of the authors. The epithelium (see fig. 213, *i*) at one or more spots, according to the number of eggs contained within the follicle, is piled up into a more or less prominent, hill-like eminence, which projects free into the lumen of the follicle—the *Discus* or *Cumulus proligerus*, *germ-disk* or *germ-hill.* In the centre of this germ-hill the egg is usually to be found; the remainder of the follicular space contains a clear fluid, the *Liquor folliculi.*

The *Tunica fibrosa* is a scanty layer of ordinary fibrous connective tissue; the very vascular Tunica propria consists of a young, richly cellular connective tissue; the cells are spindle-shaped and stellate, and among them are many round cells, resembling the amœboid corpuscles, in which, after the injection of cinnabar into the circulation, particles of the coloring matter may again be found; the transition from one layer to the other is imperceptible. In the younger follicles these layers are altogether wanting; the epithelial mass, together with the ovule, lie simply in a rounded cavity of the stroma. I have been equally as unsuccessful as Henle (50) in discovering in Mammals a structureless basilar membrane, either in the older follicles where Kölliker (59) claims to have found it, or in the youngest. With the growth of the ovule and follicular epithelium, which are embedded, as it were naked, in the stroma, a certain amount of irritation is exerted on the surrounding stroma, in consequence of which an increased vascularity will be first noticed around the somewhat larger follicles. Very soon afterwards the first trace of the subsequent Tunica propria will be seen in the shape of a ring of young connective-tissue cells surrounding the mass of epithelium. This ring enlarges with the increasing vascularity, and later its outer layers become transformed into ordinary fibrillated connective tissue. Hence the formation of the wall of the follicle seems to be directly connected with

the development of the vessels, and it readily suggests itself that a certain share in the work should be attributed to the colorless cells which have wandered thither.

The cylindrical cells of the follicular epithelium seem to be completely membraneless; their nearly elliptical nuclei are clear and transparent, and lie about in the centre of the cells. Judging from the way in which it acts under slight pressure, the protoplasma must possess great toughness and extensibility; it is easily drawn out into long threads, by means of which individual cells are connected together. Many of the epithelial cells contain fat granules; others clear shining drops, like vacuoles; while others still possess an irregular, shrunken shape; these cells, moreover, are easily broken to pieces by pressure exerted on the thin glass cover, and, by establishing under the glass a pretty strong current, they will often break up into a finely granular mass. From all these circumstances I am disposed to draw the conclusion that the cells of the follicular epithelium are gradually destroyed in the Liquor folliculi, and that the products of their disorganization contribute in a large degree to the formation of the Liquor, which we are therefore to look upon as made up of a transudation from the blood, together with the dissolved substance of epithelial cells (see also the statements of Luschka (71) on this point).

When fresh, the Liquor folliculi shows a feebly alkaline, almost neutral reaction; it is clear, or will at least become so, if allowed to stand for twenty-four hours, so that the suspended cellular detritus may have time to sink to the bottom. The albuminoid substance which it contains in solution consists almost entirely, according to my investigations, of Scherer's so-called Paralbumin (123).

In the Discus proligerus, which however only exists in the ovarian follicles of Man and Mammals, two kinds of epithelium must be distinguished: that which belongs to the follicle, and the "egg-epithelium." The latter (see fig. 213, *f*, and fig. 215 G, *a*) forms a continuous circle of cylindrical cells around the egg, in a similar manner to the epithelium of the Zona pellucida. In the younger follicles a follicular space containing fluid is not yet to be seen; the egg together with a single layer of epithelial cells completely fill the interior space. Gradually there is developed a multiple layer of epithelial cells surrounding the egg, and still later there will be observed at some distance from the egg a fissure which surrounds the latter in almost a semicircular shape, and appears to be filled with fluid; this is the first trace of the follicular space; a larger heap of epithelial cells remains closely attached to the egg, to indicate the situation of the Discus proligerus.

In regard to the situation of the egg in the follicle in Mammals, it should be mentioned that it does not appear to be constant; a number of investigators like Schrön (102) and Henle (50) would seem always to have found the Discus proligerus near the deepest portion of the follicle, where the latter is most intimately united with the stroma of the ovary, and therefore where the greatest supply of blood may be looked for. Others again, like Coste (33), locate the Discus immediately beneath the most superficial portion of the follicle. I myself have found it in both of these situations.

In describing the structure of the eggs, we may also include the eggs of the Invertebrates in our description, inasmuch as all eggs, however much they may appear to differ outwardly, are similar to each other in all their essential features.

In its first commencement every egg is a simple cell with soft, granular, membraneless protoplasma, nucleus and nucleolus; farther on in considering the subject of development we shall enter more fully into the peculiarities of

the youngest egg-cells, which I am wont to designate with His as "*primordial eggs.*" It has been customary since the discoveries of Purkyné, Von Baer, and Rudolph Wagner, to call the protoplasma of the (primordial) egg-cell the "*yolk*" (vitellus), or, according to His's recommendable designation, the "*principal yolk.*" With reference to the part it plays in the process of development—since it alone goes through with the process of segmentation—this yolk also bears the name of "*germ-yolk.*" * For the nucleus and nucleolus the terms "*germinal vesicle*" (vesicula germinativa, Purkyné's vesicle) and "*germinal spot*" (macula germinativa, Wagner's spot) are respectively used.

Already, during its stay in the Graafian follicle, the primordial egg receives about it a number of secondary formations, which must all be considered as products of the follicular epithelium. To this category belong the "*yolk-membrane*"—egg-membrane, membrana vitellina, or, as it is usually called in the egg of a Mammal, *zona pellucida*—and the *food-yolk*, or, according to His's terminology, the *subordinate yolk.* When these last-named parts have become sufficiently developed, we shall have before us the "*mature ovarian egg,*" which must then leave its resting-place, the ovarian follicle, in order to become fructified. During the passage of the mature ovarian eggs through the genital canal, the majority of them—that is to say, those in which the embryo undergoes further development only outside of the mother's body—receive a larger or smaller number of other protective membranes, to which Reichert has given the appropriate name of oviduct-membranes.

If therefore we wish to come to a clear understanding of the several component parts of the egg, and be able to make a fitting comparison between the eggs of the different classes of animals, we must ascertain the distinguishing features of the *primordial* eggs, the *ripe ovarian eggs*, and *those which are provided with the oviduct-membranes.*

In this connection it should be remembered that those structures in the ovaries of Birds, Amphibia, Reptiles, Fishes, etc., which are usually called eggs, are not such in reality, but only the Graafian follicles of these animals.

The investing membrane of the egg, the zona pellucida (see fig. 215 G, *b*) appears, under a magnifying power of moderate strength, to be a tough, transparent, homogeneous membrane, with sharp outlines on the side toward the yolk. If torn with needles its contents will stream forth, and the membrane, which displays considerable power of resistance, will then sometimes roll together; this happens for instance in the vitelline membrane of the Frog. When treated with acids, acetic acid for example, the zona is found to be very resistant, and even in alkalies it can only be dissolved with great difficulty; nothing further is known concerning its chemical reaction. With stronger magnifying powers there may be seen in the vitelline membrane of almost all living creatures a peculiar structural arrangement, which was first demonstrated by J. Müller (78) and Remak (96) in the vitelline membrane of Fishes. The membrane seems to be pierced by numerous porous canaliculi, which are arranged in radiating lines; in the Osseous Fishes these pores are very distinct, and give to the vitelline membrane a very beautiful, and—when seen spread out—shagreened appearance.

In Mammals the porous canaliculi are much finer (see fig. 215 G, *b*); I have not yet been able to demonstrate their existence in the mature egg of Birds; here, however, it is exceedingly difficult to obtain sufficiently thin

* "Bildungsdotter."—TRANSLATOR'S NOTE.

sections of the vitelline membrane; under the microscope the vitelline membrane of Birds appears to be made up of very delicate, closely woven fibrils.

The cells of the egg-epithelium, of which mention has already been made on page 516, and which in Mammals stand forth as a separate layer of the Discus proligerus, distinct from the follicular epithelium, lie in immediate contact with the vitelline membrane and are very closely adherent to it. In Birds and Reptiles the ends of the follicular epithelial cells, which are turned toward the vitelline membrane, break up into a series of very fine rods, as in the cuticular border of the intestinal epithelial cells.

In the last-named animals this basilar layer—zona radiata—is the precursor of the vitelline membrane; this layer may also manifestly be looked upon as a homogeneous membrane, traversed by numerous delicate protoplasma-threads from the follicular epithelial cells (see fig. 216). In Fishes it is an undoubted fact that from the epithelial cells delicate, hair-like processes—protoplasma-threads—are given off which enter the porous canaliculi of the vitelline membrane. I would especially recommend for these investigations the Perch's egg, in which two membranes are visible; the thick outer membrane shows these relations very distinctly, but it is also possible to make them out with a sufficiently strong ($\frac{1}{1000}$) magnifying power in the inner membrane. Pflüger (84) points to the existence of similar relations in the eggs of Mammals between the cells of the egg-epithelium and the zona pellucida. Leydig (68) has described the same thing in Insects' eggs, namely, in the egg of Timarcha tenebricosa; in the eggs of the Holothuria it has been known for a long time, so that the above-mentioned structural relations would seem to be very extensive.

The production of the vitelline membrane—a process which seems to me to be allied to the formation of cuticular membranes—must be ascribed, I think, to the follicular epithelial cells; in the egg of Mammals this devolves on those cells of the Discus proligerus which perform the functions of egg-epithelium. Probably the process is of such a nature that a portion of the protoplasma of the epithelial cells undergoes a cuticular transformation, while at the same time delicate protoplasma-threads remain fixed in the transformed mass. Already Reichert (95) and especially Pflüger (84) have in a similar manner interpreted the vitelline membrane to be a product of the follicular epithelium.

Several observers (Ransom (91), H. Meyer (76), and others) describe in Fishes and Mammals, in addition to the zona pellucida, a second very delicate membrane which lies, according to them, in close contact with the yolk, between the latter and the zona pellucida, and therefore constitutes a vitelline membrane sensu strictiori. I must confess that I have not yet succeeded in demonstrating the existence of such a membrane. Bischoff (17, 18) has expressed himself decidedly against a second vitelline membrane.—In addition to the porous canaliculi there is found in the zona of many animals a peculiar larger opening which leads to the yolk—Keber's (55) so-called *micropyle*. The same has already been demonstrated beyond a doubt in the egg of many Invertebrates, for instance in those of Insects, and then in Fishes (Bruch (25), Reichert (93)). In Insects the immediate neighborhood of the micropyle is often covered with the most tasteful markings, which at once give a prominence to the spot in the vitelline membrane (see the descriptions of Leuckart, 66). In Fishes also, as Buchholz (24) for instance has shown in Osmerus eperlanus, peculiar appendages are sometimes seen arranged around the micropyle. The latter originates in Insects at that point where the egg-cell communicates with the so-called yolk-forming cells (see farther on and Fig. 217). Pflüger (84) has described in the eggs of Cats larger openings, in one of which lay one of the cells of the Discus, one-half of which was already within the zona, while the other half was still outside in the egg-epithelium—twin-cells, stopple-cells (Pflüger); in other instances he saw processes of the cells of the

egg-epithelium penetrating deep into the substance of the zona. These observations have not yet been verified by others.—Where a micropyle exists, its office always seems to be to afford the seminal threads a passage into the interior of the egg.

The principal yolk has no different characteristics from an ordinary cell-protoplasma. Even contractility has recently been observed in it by Pflüger (84), Von La Valette (117), and Stricker (114). It is a remarkable circumstance that, with perhaps the exception of some ganglion-cells, the egg-cell, even exclusive of the subordinate yolk, possesses the largest collection of cell-protoplasma around one nucleus, of which we have any knowledge; in other words, the egg-cells belong to the largest singly-nucleated cells. The egg protoplasma is very granular, even when in a fresh condition; His (53) describes in it a number of small granules, which by their reaction show themselves to contain protagon, and which are termed by him true vitelline granules, in contradistinction to the granular elements of the subordinate

Fig. 215.

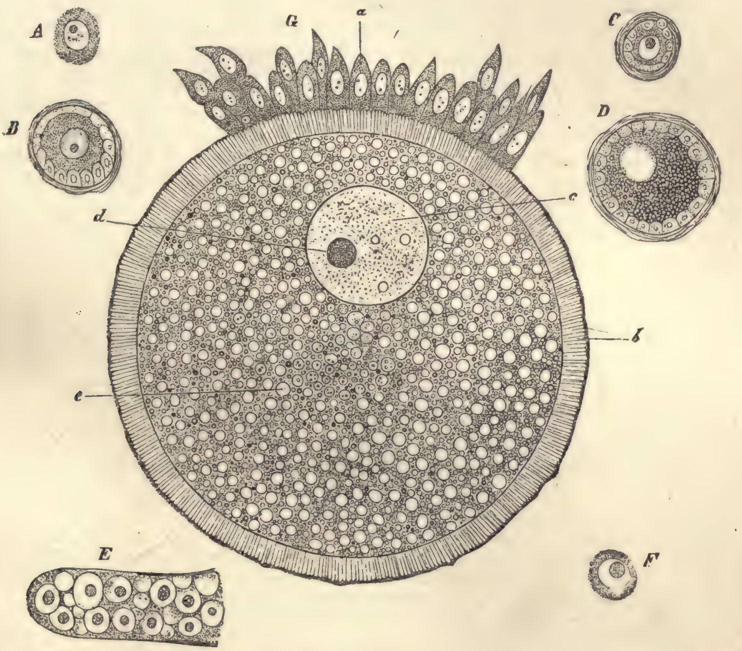

Fig. 215. *A*. Primordial egg of the Human being; 8 months' fœtus (Hartnack $\frac{8}{9}$). *B*. Primordial follicle of the Rabbit. *C*. Primordial follicle of a Dove. *D*. A somewhat older follicle of the same animal; commencement of the formation of the subordinate yolk. *E*. Blind end of the ovary of an Ascaris nigrovenosa. Germinal vesicles (some of which possess a germinal spot and Schrön's "granule") in a diffuse mass of protoplasma. *F*. Egg of the Ascaris nigrovenosa from about the middle of the ovary; Schrön's granule; commencement of the deposition of yolk-matter. *G*. Egg from a follicle (2 mm. in diam.) of the Rabbit. *a*. egg-epithelium; *b*. striated zone with radiating striæ; *c*. germinal vesicle; *d*. germinal spot; *e*. yolk. B—G. Hartnack $\frac{8}{3}$.

yolk. In the younger Mammalian egg these granules are found of the most varied sizes; the largest (see fig. 215 G, *e*) are perfectly spherical vesicles, similar to the vitelline spherules of Birds; as is represented in the

last-mentioned figure, they lie scattered among the smaller granules, and shine through the mass which these compose. At a later period they become so much more numerous and so brilliant that besides them almost nothing else can be seen within the zona. According to their microchemical reactions they must be classed among albuminoid bodies.

The germinal vesicle lies embedded somewhat eccentrically in the substance of the principal yolk; it is shining, transparent, circular, with sharp contour, and large in comparison with the cell. These large shining nuclei are at first a very striking characteristic of the egg-cells. I myself have thus far seen but one nucleus in each egg-cell; Kölliker (59) gives a drawing of a young egg-cell with two nuclei; in the mature egg it seems that a double germinal vesicle has never yet been observed.

In the primordial eggs the nucleolus—the macula germinativa—is never wanting. It usually has a dull shining or finely granular appearance, and seems more like a solid body, as I should be inclined, with Von La Valette (117) to believe it, although Schrön (103) has described it as a vesicle. On the addition of distilled water the germinal spot disappears (Von La Valette, 117). Two germinal spots in the same germinal vesicle have already often been described; as for instance by R. Wagner in the Cockchafer (Geschichte der Zeugung und Entwickelung, Abhandl. der bayrischen Akad. d. Wissensch. Bd. ii. 1837), then by Von La Valette (117) in the larva of the Dragon-fly, and recently by Claparède in the Earthworm, where it seems to be the rule. In the latter case the two germinal spots, one of which seemed always to be larger than the other, were found united into a double spot (see Zeitschrift. Wiss. Zool., 19. Bd., 1869, S. 563).

In addition to the germinal spot there are likewise found in the germinal vesicle small round corpuscles, whose exact meaning has not yet been ascertained. If with Von La Valette (117) and Pflüger (84) we look upon the germinal spot as a deposit originating from the germinal vesicle, then must these corpuscles be interpreted as of similar origin. In Mammals only does the germinal spot continue to exist in the mature eggs: in all other Vertebrates it disappears already at a very early period, and in its place there is found in the germinal vesicle a cloudy, finely granular mass, which, in the Batrachia and Osseous Fishes, for instance, is filled with a number of shining spherules; the exact time of the disappearance of the germinal spot cannot be stated.

Schrön has recently described in the germinal spots an extremely small, shining, apparently solid corpuscle, to which he gives the name of "granule" (Korn). In Mammals I have not yet been able to find it, whereas in many of the lower animals, the Ascarides for instance, it is constantly present; perhaps, however, it may be interpreted as the smaller portion of Claparède's double spot (see fig. 215, E. and F.). Von La Valette (117) considers Schrön's granule to be a vacuole, but at the same time is unable to make out anything permanent about its structure. Balbiani (9) goes the farthest in his statements concerning the structure of the germinal spot. He describes contractile vacuoles inside of the germinal spot, which itself is also contractile. According to him there is given off from the germinal spot a hollow, canal-shaped process which fits into a similar canal of the germinal vesicle; and finally the vacuoles of the germinal spot communicate with the tubular process of the latter.

Hitherto it has been pretty generally accepted that the mature Mammalian egg was nothing else than a fully-grown primordial egg; more recent observations and interpretations, to which I would gladly give my assent, lead us, however, to conjecture with strong probability that in the mature Mammalian egg there is present a certain amount of subordinate yolk besides the principal yolk. Pflüger (84) for instance has taught us of the existence of two different elements in the yolk of Mammals, one of which, in young eggs, more transparent, immediately surrounds the germinal vesicle, while the other, more opaque, appears like a peripheral layer of the first. It seems most natural to interpret the peripheral portion of the yolk as a formation of later

date, originating perhaps from the follicular epithelium. This circumstance is of the greatest importance in its bearings on the question of the comparative anatomy of eggs.

Hitherto it has caused investigators considerable trouble to interpret the component parts of Birds' and Reptiles' eggs. Simple inspection of the mature ovarian egg reveals to us a yellow mass of considerable size—the *yellow food-yolk*, surrounded by a thin spherical shell of white yolk material —the *white food-yolk*, and the whole invested with the vitelline membrane. When the egg is held still in a position of equilibrium (see J. Oellacher in Stricker's "Studien aus dem Institute für experimentelle Pathologie in Wien," Wien, 1870, Taf. ii., Fig. 1) we shall always find floating on the top, immediately beneath the vitelline membrane, a whitish spot, varying from 3 to 4 millim. in diameter—the *Cock's tread* or *Cicatricula ;* this is the principal yolk with the germinal vesicle. If we examine these relations in an egg taken from beneath a setting hen, then if—as is usually the case—the egg has been impregnated, the process of segmentation will have already been completed, and we shall see before us in this spot the *subdivided germ-disk.* The white yolk surrounds the principal yolk on all sides, and also dips down like a slender thread into nearly the centre of the yellow yolk, where it forms a spherical swelling the size of a pea—the Latebra or *Vitelline cavity* of Purkyné.*

The principal yolk with the germinal vesicle does not present any special peculiarities apart from its dimensions and the early disappearance of the germinal spot; it represents the primordial egg; in the Bird's egg the principal difficulty lies in the question concerning the origin of the food-yolk and its relations to the primordial egg-cell.

In reference to the historical part of this question it may be stated here in brief that, since the discovery of the Mammalian egg by Von Baer, two conflicting views have been held concerning the Bird's egg: the first, which is supported by Schwann (104), Gegenbaur (43), Leuckart, Kölliker (58), and Cramer (34), considers the Bird's egg as an entity, as a single cell; while the other, supported by H. Meckel (73), Allen Thompson (115), Ecker (37), Stricker (114), His (53), and others, assumes that the food-yolk, as well as the vitelline membrane, is a secondary deposit—the product of the follicular epithelium. Another point of controversy relates to the nature of the component parts of the food-yolk, which Schwann (104), and Klebs (56), and recently His (53), have declared to be cells, whereas by others, Gegenbaur (43), and Stricker (114), for example, they are looked upon as spherical, drop-like bodies of a peculiar kind, which can lay no claim to the dignity of a cell, but should rather be classed with the colloid spherules, albuminous drops, etc., which are found in secretions.

The youngest Birds' eggs are entirely like those of Mammals (see fig. 215, B. C. and D.) excepting that the follicular epithelium, contrary to the views of His (53), consists of but one layer. Soon an increase in the contents of the follicle will be noticed, although a fluid analogous to the Liquor folliculi will never be found there, but in its stead a finely granular mass which surrounds the principal yolk, but yet is distinctly separable from it; this is the first foundation of the subordinate yolk; at the same time the principal yolk remains essentially unchanged. The older the follicle, the larger will the small granules of the subordinate yolk appear; they soon assume the shape of shining, angular bodies and then of small spheres, which appear perfectly homogeneous and in which no membrane can be demonstrated—for

* The term "cavity" is used because in boiled eggs this spherical white mass of yolk does not usually become solidified, but remains fluid, so that we seem to have before us a real cavity filled with fluid.

certainly we would not be justified in considering that tunicle, which, after the addition of water, becomes visible in the larger spheres, as the equivalent of a cell-membrane. These small, angular, and round vitelline bodies are very resistant; when crushed by pressure on the thin cover, the ruptured surface assumes a radiated, stellate form; their chemical reactions, which have very recently been investigated by His, place them among the protagon-containing substances. Finally, these spheres attain quite considerable dimensions, but the transition may be followed step by step from the smallest vitelline bodies to the largest vitelline spheres. In the larger spheres there are found almost always one or more of the smaller bodies, and still smaller bodies will frequently be found lying inside of the latter. It was chiefly owing to this circumstance that His (53) interpreted the vitelline spheres as cells, for he considered the bodies enclosed within them to be respectively nuclei and nucleoli. Their form, the inconstancy of their appearance, their solid consistency, the gradual transition from the smaller to the larger spheres, and the circumstance that the older the follicle, the smaller on the one hand will be the number of the small spheres, while on the other the larger ones will be more numerous, will not permit me to side with him in this interpretation. Just as little, however, can I side with Gegenbaur in the belief that the smaller spheres are an endogenous production of the larger ones; I consider it much more probable that the smaller spheres are simply forced by pressure into the larger ones, inasmuch as the larger spheres are much softer than the smaller ones, and in every motion of the yolk its closely-packed component parts must press upon each other. The larger spheres appear to grow from the smaller elements simply by swelling. Von Wittich (128) has made similar statements in reference to the yolk of the Arachnidan egg; here the vitelline spheres are not cells: they grow by imbibition of the fluid albumen which surrounds them. The yellow yolk, which constitutes later the chief portion of the Bird's and Reptile's egg, is simply a modification of the white; it contains chiefly the larger vitelline spheres, whose substance, however, is clouded by the presence of fine molecules; what the origin of this opacity is, has not yet been made a subject of investigation.

But finally, whence originates the finely granular mass which composes the subordinate yolk? It is indisputably a product of the follicular epithelium—nothing less than a metamorphosed protoplasma of the follicular epithelial cells. Although I agree with Gegenbaur's views on most points, on this one I must differ from him (45), especially as he has recently given prominence to his former statement, that the component parts of the yolk are simply modifications of the protoplasma of the primitive egg-cells. In young eggs no boundary-line can be seen between the protoplasma of the epithelial cells and the finely granular subordinate yolk; it seems as if while the protoplasma issued forth from the inner membraneless end of the cells, and became lost in the substance of the subordinate yolk at the nuclear end of the epithelial cells—that which is nearest to the wall of the follicle—new protoplasma were constantly forming and pushing forward to supply the place of the old. However that may be, the follicular epithelium is at all events directly connected with the formation of the subordinate yolk; this follows from two circumstances. In the first place there are found, in Lizards, for instance, in the protoplasma of the epithelial cells, quite small shining bodies, similar to the youngest vitelline granules; and then, in the next place, the follicular epithelial cells (see fig. 216) are most fully developed at the time when the formation of yolk is taking place most actively. Meckel von Hemsbach (73), Allen Thompson (115) and

others have already expressed views which accord with the above. The radiated layer (see fig. 216) between the follicular epithelium and the yolk cannot offer any obstruction to this mode of growth, for it is, as I have already mentioned before, traversed by numerous porous canaliculi, in which delicate protoplasma-threads of the epithelial cells are lodged.

The same relations exist in the eggs of the Selachia, as Gegenbaur's (43) investigations, for instance, have shown. I also find the same kind of egg-formation in the Osseous Fishes and the higher Crustacea, as for example Astacus fluviatilis, whose vitelline plates and spheres originate in precisely the same manner, and in whose eggs a principal and subordinate yolk may be clearly distinguished, as in the case of Birds. As a radical distinction between the principal and subordinate yolks, S. Stricker (114) has made the beautiful discovery in the egg of the Trout, that under favorable circumstances amœboid motions may be seen in the former, whereas the latter remains entirely passive.

Fig 216.

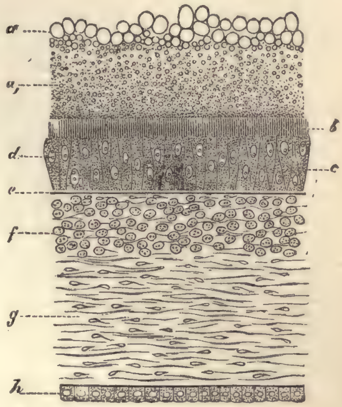

Fig. 216. (No. 25, Plate III. of my book.) Section of the wall of a Hen's follicle (4 mm. in diam.). Hartnack $\frac{3}{7}$; *a*, vitelline spheres; a_1, molecular vitelline layer; *b*, zona radiata; *c*, follicular epithelium; *d*, epithelial cells with delicate hairs at their basilar extremities; *e*, membrana propria folliculi; *f*, inner, highly cellular layer of the connective-tissue wall of the follicle; *g*, outer layer; *h*, ovarian epithelium.

In the Batrachian eggs, although in other respects they resemble very closely those of the Osseous Fishes, no distinct separation can be made out between the principal and subordinate yolks; here again the relations are more like those of Mammals. Nevertheless many things —as for example the formation of the vitelline plates, which are entirely analogous to those of Fishes—favor the view that here also a subordinate yolk is produced by the follicular epithelium, although optically it cannot be distinguished so easily from the mass of the principal yolk. Farther on I shall allude to the doubts which might be raised against this view from the fact of the complete subdivision of the Batrachian eggs.

The above-mentioned *vitelline plates*, which are to be found in the eggs of Turtles, Batrachia, Cartilaginous Fishes and many of the Osseous Fishes, are doubly refractive crystals (Radlkofer) of an albuminoid substance, which W. Kühne (Lehrbuch der physiologischen Chemie, S. 552) declares to be Vitellin. Virchow (119) was the first to demonstrate by micro-chemical reactions their albuminoid nature, and showed that at all events they were not a fatty substance, which they were previously believed to be. The form of the crystals varies in the different species: in Rana, for example, they are quadratic tablets whose angles are often drawn out to a point, whereas in Perca the forms are very variable, approaching, however, most commonly, the spherical form in the mature eggs. In reference to this point see especially Radlkofer's work in the Zeitschrift für wiss. Zoologie, Bd. 9—"Ueber die wahre Natur der Dotterplättchen."

I will add to these remarks on the eggs of Vertebrates a few words concerning the ovary and eggs of Invertebrates.

Luberkühn's (69) observations on the Porifera, Balbiani's (8) and Stein's (110) investigations concerning the Infusoria, Greef's (48) and Strethill Wright's (112, 113) statements relating to the Rhizopoda have thrown some light on the relations (here under consideration) which exist in the Protozoa; nevertheless our knowledge in this department is exceedingly deficient. In the Porifera the eggs do not go through the process of development in special organs, but individual epithelial cells (?) of the walls of the canalicular system, which traverses the spongy body, may develop into eggs. In the Infusoria first, according to Balbiani's discovery, is there found a special organ for female germs—the so-called *nucleus*. This nucleus has a very variable shape—round, oval, or even band-shaped; its granular, protoplasma-like contents, after fructification has been accomplished by the conjugation of two Infusoria, break up by a sort of segmentation-process into several subdivisions, and it is still a question whether the nucleus is to be considered as a single egg or these products of subdivision as eggs; or, in other words, whether the nucleus is to be looked upon as an ovarium, consisting in that case only of germinal matter without any intervening substance to serve as a framework. Our knowledge concerning the female germs of the Rhizopods is the most deficient of all; the few statements made by the above-named authors in relation to this question lead us to infer that the eggs here are enclosed in a structure similar to the nucleus of the Infusoria.

Already in the *Cœlenterata* distinct special organs are found for the production of the eggs, which in the higher forms—*Actinia*, *Ctenophora*, etc.—possess a follicular shape. It is supposed that the eggs originate from the cells which line these follicles. As a rule, the capsules of the eggs appear to be appendages of the gastro-vascular apparatus, in the form of numerous diverticula of the same; for, as is well known, in these animals the generative masses are also discharged into the cavity of the stomach or into one of its radiating subdivisions.

The ovaries of the Echinodermata consist of rounded or oblong sacs which are usually united into several gland-like groups; the number and arrangement of these groups correspond to the radiating segments of the body. In the higher forms, as for instance in the Holothuria (see the work of E. Selenka (105), the individual glandular sacs empty into one or more outlet ducts. The eggs lie closely packed in the glandular sacs; their mode of development, however, is yet a matter for further and more accurate investigation. When mature they possess a thick vitelline membrane, which is striated in a radiating direction, and an aperture which is to be interpreted as a micropyle (see page 518).

From the discoveries of Meissner (75), Bischoff (Zeitschrift f. wiss. Zoologie, Bd. vi.), Munk (81), Leuckart (67), Hering (51), Claparède (27, 28), and others, as well as from my own study of the subject in the Ascarides, I am able to give the following account of the ovaries of Worms. The ovary proper is either a vesicular organ, provided with a special outlet duct which terminates in the intricately-built sexual canal, or else, as in the Ascarides, it occupies the blind extremity of the genital tube. Inasmuch as in many Worms, the parasitic, for example (Trematoda, Cestoidea), other special glands exist which since the time of Von Siebold have been called "yolk-stocks," so here the ovary proper is distinguished as the "germ-stock." As regards the function of these two glandular apparatuses, which undoubtedly produce the egg, the germinal vesicles with the germinal spots are clearly formed in the germ-stock. And furthermore there is always found, as Bischoff has already stated, between the germinal vesicles and sur-

rounding them, even at the very end of the germ-stock, a certain amount—small it may be—of finely granular Protoplasma, and the nearer the eggs approach to the outlet of the germ-stock the more distinct becomes the halo of Protoplasma surrounding each germinal vesicle, and each egg then appears as a completed cell possessing Protoplasma (yolk), nucleus, and nucleolus; consequently the eggs of the germ-stock might properly be compared to the primordial eggs of Vertebrates. It has been stated by many that in the germ-stocks only germinal vesicles were formed, while the entire yolk-protoplasma originated in the yolk-stocks. I cannot agree with this statement, for, with Gegenbaur (45, page 287), I find a delicate halo of Protoplasma attached to every egg already at the time of its leaving the germ-stock. The morphological meaning, moreover, of the yolk-stocks is not yet definitely determined; Gegenbaur (45) suggests that "they may be considered as portions of a sizable ovarium, only a very small portion of which remains as such, while the largest part of it undergoes a retrograde metamorphosis into yolk-stocks." However that may be, there are at all events produced in the germ-stock—the true ovary—completed cells, similar to the primordial eggs of the Vertebrates. Observations of Streda (Reichert's und Du Bois-Reymond's Archiv, 1867, p. 52), G. Walter (124) and Leuckart (67), which I have been able to verify in Ascaris nigrovenosa, show that the eggs are developed from the epithelial cells of the ovarian sacs; at all events the greatest variety of transition-forms are found here, and, at the very end of the ovary, the youngest egg-cells and epithelial cells can no longer be distinguished one from the other. As the eggs in the genital sacs of the Ascarides push their way onward, the granular yolk-mass surrounding the germinal vesicle increases in quantity, and later there is formed around it a thinner or thicker vitelline membrane. The increase in granular yolk-material is evidently—as may be gathered from Leuckart's (67) and my own observations—only a product of the epithelium, which lines these parts of the genital sack. I must limit myself here to this short description, in which I have brought forward especially such facts as would be of service in comparing the egg-formation in Worms with that of the higher animals. It would also be out of the question for me to enter into a description of the various forms of ovaries, and the relations of their outlet tubes in the so numerous species of Worms.

All Mollusca possess for the production of the egg well-developed glandular organs, consisting of a number of acinous follicles, whose epithelial cells may become transformed into eggs. The so-called "hermaphrodite gland" is very extensively found throughout the Molluscous type; in it, even sometimes in the same follicles, both eggs and seminal corpuscles are formed; their immediate origin is, as Eisig (Zeitsch. f. wissensch. Zoologie, Bd. 19) has recently described it in Lymnæus auricularis, in the epithelial cells of the glandular acini. Both generative elements then seek an exit through the same outlet channel. From what I have seen in the Helix and Limax, the larger eggs which are attached to the walls of the acini are shut off from the rest of the cells by a special delicate capsular membrane; I was not successful in investigating more accurately the formation of this capsule, nor in demonstrating the existence of an epithelium on its inner surface, which would render this capsule entirely analogous to the Graafian follicle of a Vertebrate. With reference to the formation of ova in the Mollusca, consult the works of Semper (106), Claparède (29), Baudelot (11), Eisig and others.

In the Arthropoda, which, I believe, rank next to the Vertebrata as regards the development of their female sexual organs, structures are found which correspond perfectly to the Graafian follicles.

Fig. 217 represents in a semi-diagrammatic manner a portion of the tubular egg-sac of Vanessa urticæ; in the narrow portion *a* is the termination of the tubular ovarium, which is attached to the dorsal vessel by a slender

Fig. 217.

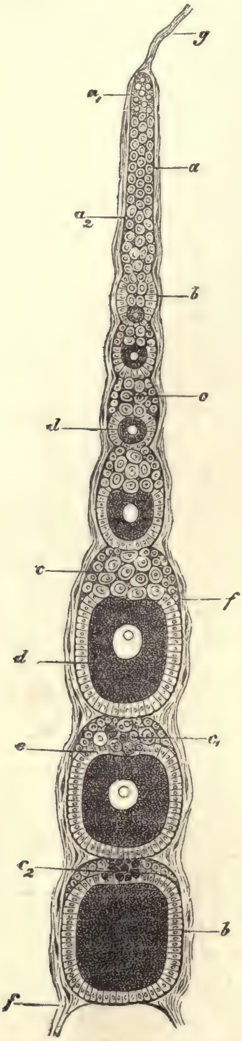

Fig. 217. Egg-tube of Vanessa urticæ; semi-diagrammatic. (A large part of the egg-follicles are left out, in order that the various stages of development may be brought together in a single figure.) *a*, blind, tubular termination of the ovary containing at a_1 germinal vesicles in a diffuse mass of Protoplasma, and at a_2 already fully-developed cells; *b*, *b*, egg-follicles; *c*, *c*, yolk-forming cells, which at c_1 are in the process of degeneration; c_2, granular mass, the remains of the yolk-forming cells; *d*, *d*, eggs; *e*, location of the subsequent micropyle; *f*, connective-tissue external wall of the egg-tube; at *g*, this connective-tissue sheath is continued on to the Dorsal vessel. × circa 100.

cord, g, of connective tissue. Within the ovary at its extreme end a_1, clear germinal vesicles with nuclei will be found embedded in a diffuse, soft mass of Protoplasm, in exactly the same manner as in the egg-sacs of the Ascarides; farther down, at a_2, we shall see a portion of these elements—each of which by this time possesses its separate mass of Protoplasm—lining the walls of the egg-sac as epithelial cells, while other cells of exactly the same size and shape occupy the axis of the tube. Still farther down a few not only of the central but also of the parietal cells become somewhat more prominent than the rest by their size, and especially by the greater size and brilliancy of their nuclei; they approach more and more to the centre of the tube, and then will be found in groups of from 6 to 8 and more, enclosed in wreath-shaped distentions of the wall of the tube. Soon we find subdivisions of the egg-tube as at b, in whose centre lie a number of primordial egg-cells, while the parietal cells assume distinctly the character of follicular epithelium—for we certainly can look upon the several sections of the wreath as follicles. Farther on, however, the picture changes; one of the egg-cells, that one always which lies the deepest, increases more rapidly in size, retains its very much enlarged nucleus, while at the same time its Protoplasma becomes darker; the nuclei of the remaining primordial egg-cells remain smaller, and finally, together with their cell-protoplasma, undergo granular degeneration. At the same time the larger egg-cell becomes shut off from the other cells by a bending inwards of the epithelium. Thus two subdivisions are produced in the follicle which are distinguished from each other by the names of yolk-compartment and germ-compartment. Since the time of Lubbock (70), whose view most modern authors have adopted, it has been customary to call the degenerating upper egg-cells "yolk-forming, cells," for it was supposed that these cells were specially destined to furnish the definitive egg-cell with its yolk-material. A cord-like formation, which in many Arthropoda, the Coccida (Claus, 30), for example, connects the yolk-forming cells with the egg-cell, gave material support to this belief. As for myself I cannot accept this interpretation. In the first place, I find in the yolk-forming cells only manifestations of fatty degeneration and decay, whereas the mass of yolk in the definitive egg goes on growing long after the yolk-forming cells have been destroyed. I consider the mass of yolk, therefore, at least the largest part of it, as a product of the follicular epithelium, to which source also must be ascribed the formation of the vitelline membrane, which in Insects is often marked with a very beautiful design. The micropyle is formed at that pole of the egg which faces the yolk-compartment (see fig. 217). The structure of the ovaries in most Insects, so far as we are acquainted with it from the works of Stein (Vergleichende Anatomie and Physiologie der Insecten, I. 1847), H. Meyer (77), Weismann (125), Claus (30), Leydig (68), Lubbock (70), Landois (62, 63), Bessels (14), and others, is the same as in the Vanessa urticæ.

I have already mentioned that in the higher Crustacea the eggs are formed in special follicles; in the lower forms the ovaries are simpler in shape, either tubular or like sacs. The ovaries and eggs of the Araneides, concerning which we have received from Von Wittich (127, 128) an exhaustive report, present certain peculiarities. The follicles consist of lateral pouches of the tubular ovarium; according to the statements of Von Wittich they possess an epithelium only in the short neck-piece which joins it to the main tube; at all events it is at this very portion of the follicle that later the vitelline molecules accumulate. At first no germinal spot can be seen in the germinal vesicles, although a small mass of protoplasm, to

judge from Von Wittich's drawings, is always present. The germinal vesicles lie at first close to the wall of the ovarian tube, and by their own growth—while at the same time the surrounding cellular protoplasm increases—cause it to pouch outwards; in this manner the follicles are produced. Here also (see fig. 192 A of Von Wittich's work) the primordial eggs can probably be looked upon as originally epithelial cells of the ovarian tube. The so-called yolk-kernel, which is always found by the side of the germinal vesicle in the eggs of certain species of Araneides, and which was first discoved by Von Wittich, is a very peculiar object, spherical in shape and composed of concentric layers; it is probably similar in nature to the bodies of the same name in the eggs of the Batrachia and Osseous Fishes. In the Batrachia the yolk-kernel disappears in the older eggs (Allen Thompson), whereas in the Araneides the central portion of this body becomes later fluid, while the peripheral portion remains as a firm capsule. The significance of the yolk-kernel is thus far unknown.

Development of the Ovaries and Eggs.—In the Fowl's embryos, no matter to which sex they belong, the first traces of the germinal glands are noticed about the end of the fourth day. About this time the Wolffian body is covered with a regular cylindrical epithelium, while the remainder of the peritoneal cavity is lined already with small flat cells.

Through the work of Schenk (101) we know that originally the entire pleuro-peritoneal fissure is lined on its inner surface with cylindrical cells which originate from the subdivided lateral portions of what was at first the middle germinal plate. Schenk assumes that this layer of cells, which corresponds to the "cutaneous and intestinal fibrous plate" of Remak,* serves exclusively to form the subsequent peritoneal epithelium. Götte (47) has recently adopted this view in reference to the Batrachia. Throughout the greater part of the peritoneal cavity these cylindrical cells very soon disappear, and in their place appear entirely flat, pale elements; only the median angle—corresponding to Remak's middle plate—and later the Wolffian body, which grows out from this spot, retain their covering of cylindrical epithelium.

From the fourth day on, the above-mentioned epithelium undergoes a decided thickening, both along the median and on the lateral side of the Wolffian body; the median thickening is the first foundation of the ovarium, while from the lateral will be formed the subsequent Tuba—Müller's duct.

The thickening of the epithelium also shows itself first, in male embryos, at the locality of the germinal gland; here, however, it disappears towards the eighth or ninth day, whereas in the female embryos it grows constantly thicker.

Very soon a small, spherical growth, rich in cells, will be seen pushing its way up from the interstitial tissue of the Wolffian body beneath the epithelial thickening just mentioned (see fig. 218). *The thickened epithelium above it now gradually becomes so disposed as to form the foundation for the Graafian follicles and eggs, and also for the subsequent ovarian epithelium,* whereas the connective-tissue growth is destined to constitute the vascular stroma of the ovary.

Already in the ovaries of Fowls' embryos, which are 4–5 days old, the interesting observation can be made, that among the epithelial cells a few are prominent by their size and rounded form, and by the magnitude of their nuclei (see fig. 218 O). From the regularity in shape of these formations and from the constancy of the locality in which they are found, it

* Haut- und Darmfaserplatte.—Translator's Note.

may safely be inferred that these are in fact very young primordial eggs, which have become developed already during embryonic life, by simple growth from the germ epithelial cells. The relations we have just described may also easily be verified in Mammals (Dogs' and Rabbits' embryos).

The further development of the ovaries consists in a peculiar process of intergrowth, in which both the superficial epithelium (germ-epithelium) and the vascular stroma lying beneath it, participate (fig. 219 will give some idea of the process). While a few vascular shoots of connective tissue, some delicate, others larger, grow upwards from the Stroma, the epithelium also increases in amount by new productions; in this way the trabeculæ of the Stroma, by insinuating themselves between the epithelial cells, will enclose a smaller or larger number of them, until little by little the cells become embedded in the depths of the vascular Stroma. These connective-tissue shoots may be seen at *c* in fig. 219; and at *d*, *d*, embedded masses of epithelial cells, or such as are on the eve of being embedded, are visible. It is clear from the nature of this process that of these individual masses of epithelium the largest part must be connected together like the cords of a net, and hence that at this period of its development the ovarium will represent a system

Fig. 218.

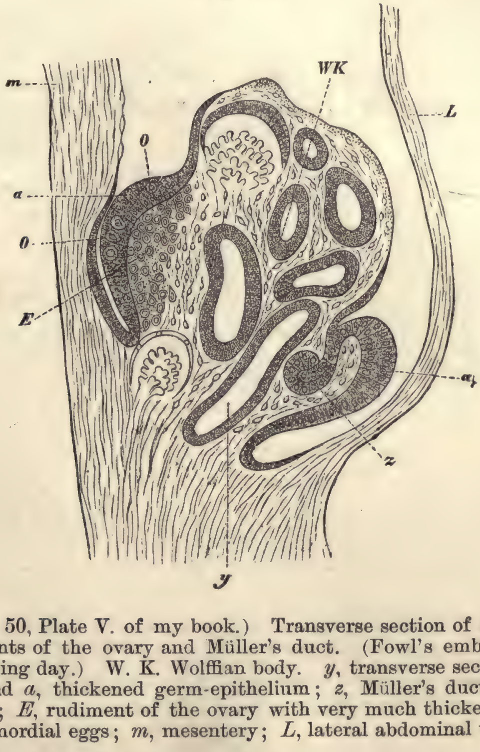

Fig. 218. (Fig. 50, Plate V. of my book.) Transverse section of the Wolffian body with the rudiments of the ovary and Müller's duct. (Fowl's embryo at the end of the fourth hatching day.) W. K. Wolffian body. *y*, transverse section of the Wolffian duct; a_1 and *a*, thickened germ-epithelium; *z*, Müller's duct connected with germ-epithelium; *E*, rudiment of the ovary with very much thickened germ-epithelium; *O*, *O*, primordial eggs; *m*, mesentery; *L*, lateral abdominal wall.

of trabeculæ composed of vascular connective tissue, whose meshes communicate with one another like the spaces in a cavernous tissue. His (52) and Kölliker (59) have already called attention to this cavernous structure of the fœtal ovary, nevertheless they did not understand its development. Kölli-

ker moreover states quite rightly that the individual follicles are formed from the masses of epithelial cells—"glandular trabeculæ" as he calls them (ovum-trabeculæ, Frey)—by a progressive growth of connective-tissue septa which insinuate themselves between the cells.

Among the embedded epithelial cells very many will now stand out from the rest by their size and the magnitude of their nuclei, just as we have already seen it, and may even yet at this period of the development see it in the superficial epithelium (see fig. 220). Pflüger (84, p. 113) has already made mention briefly, in his third preliminary communication, of such very young egg-cells in the ovarian epithelium of young Cats, and designates them expressly as "prospective eggs;" * in his completed work, however, he has not followed up the subject any farther. Other cells remain small and surround the individual egg-cells—that is, the larger cells—after the manner of an epithelium. It is easy, moreover, by a comparison of the younger ovaries with those that are older, to prove that the connective-tissue Stroma between the embedded epithelial balls increases steadily, pushing its way between the individual egg cells thus covered with epithelium. In this manner each epithelial ball will soon be converted by the growth of these vascularized bands into just so many separate compartments

Fig. 219.

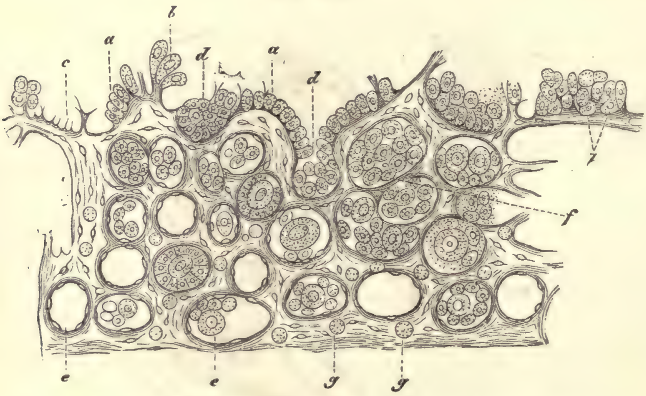

Fig. 219. (Fig. 11, Plate II. of my book.) Vertical section of the ovary of a 32 weeks old Human fœtus; Hartnack $\frac{3}{7}$. *a*, *a*, epithelium; *b*, *b*, youngest egg-cells of the epithelial stratum; *c*, trabeculæ of connective tissue, pushing their way forwards into the epithelial layer; *e*. *e*, primordial follicles, surrounded by an outline of narrow connective-tissue cells; *f*, groups of already embedded epithelial cells (egg-balls), among which are a few larger cells (primordial eggs); *g*, grain-cells of His.

as there are egg-cells in the ball; later there may be found follicles containing two or more eggs, but such an occurrence is rare (see fig. 213). I need scarcely add that the compartments which have thus been produced are the youngest follicles—the primordial follicles.

The form of the compartments in which the egg-cells together with the follicular epithelium are embedded, is very variable; the rounded and oval alternate with oblong, tubular formations (see fig. 220), and the latter become of course more

* "Evidente Eier."—Transl. Note.

prominent, the more the interstitial stroma-tissue increases in amount. In Human embryos of the 4th to the 7th month, the rounded compartments predominate, whereas in new-born infants, and in children during the first years of their life, the elongated epithelial sacs will be found in greater numbers. The elongated tubular formations in the ovary, the ovarian tubes, would seem therefore to be secondary formations, which depend rather on a certain prolific development of the interstitial connective tissue, and are not, as Pflüger (84) would have us believe, necessary fore-steps to the formation of the Graafian follicles. Pflüger in his account lays the greatest stress on these ovarian tubes. He has described (84) them as possessing a structureless membrana propria, by whose successive constrictions the individual Graafian follicles are formed. I have not yet succeeded in demonstrating such a membrana propria; His (52), too, and Langhans (64), as well as Kölliker, are unable to find it; as already mentioned, it is wanting in the follicles of Mammals, but at a later stage it is found in the larger follicles of Birds (see fig. 216). When the follicles become separated by constriction, the egg-cells, according to Pflüger, still remain connected for a time through the medium of their protoplasma; the spot where this occurs—the pole of the follicle—is recognizable even after the constriction is complete, by the diminished size of the epithelial cells.

Moreover, according to Pflüger's (84) representations, the tubes which are situated close to the surface of the ovary end blind, and in this blind termination the germinal vesicles are produced. The protoplasm at first surrounds the germinal vesicles diffusely, but afterwards, when they push their way deeper down in the tube, it

Fig. 220.

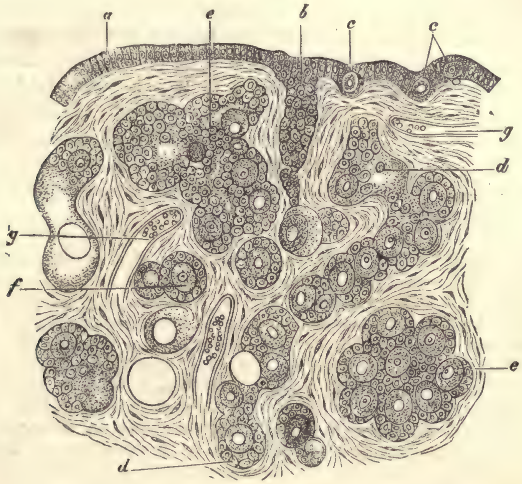

Fig. 220. Portion of a sagittal section of the ovary of a new-born child. (Hartnack $\frac{3}{7}$ with tube pushed in). *a*, ovarian epithelium; *b*, rudiment of an ovarian tube; *c*, *c*, eggs embedded in the epithelium; *d*, *d*, long ovarian tube in the process of transformation into follicles; *e*, *e*, egg-balls, likewise in the process of transformation into follicles; *f*, youngest, already isolated follicles; *g*, *g*, vessels. In the tubes and egg-balls the primordial eggs can be distinguished from the smaller epithelial cells, which constitute the subsequent follicular epithelium.

surrounds each germinal vesicle more distinctly. A number of these cells will also soon grow more actively, while the others remain in statu quo, and represent the epithelial cells of the tubes. The larger cells, the primordial eggs, occupy the centre of the tubes. The eggs, whose mode of origin reminds one perfectly of what has already been said of the Nematoda and Arthropoda, are called by Pflüger "primitive eggs." Afterwards these multiply, he says, by subdivision and budding, and the products of these processes of subdivision are definitive eggs, which, however, remain still for some time connected together in the tubes by protoplasma-processes, after the fashion of a chain (Pflüger's egg-chains). The most important factum in

this account, which is now pretty generally accepted—the multiplication of the primitive eggs—I have not been able to see; I must also, from what I have already said, deny the origin of the primitive eggs and germinal vesicles in the blind termination of a tube. Pflüger, moreover, has represented in one of his figures (Tab. III., Fig. 1) a connection between one of the tubes and the superficial cylindrical epithelium of the ovary, and has often expressed the view that the contents of the egg-tubes might originate in the ovarian epithelium, although at the same time he persists in considering the latter as a serous epithelium; finally, however, he returns again to the mode of formation we have just described, whereby the eggs are formed in the blind ends of the tubes, and lays the greatest stress on this point.

Bischoff and others have expressed the view that the development of the egg ceases with the termination of the fœtal period, and from my own researches I must agree with him on this point. Pflüger undertook the first to demonstrate a post-embryonic new formation of egg-tubes, occurring as he believed periodically; in this view he was supported by Kölliker, who (Gewebelehre, page 560) believes that the formation of new follicles and eggs takes place by the proliferation of the epithelium of already existing follicles. I do not deny that even in adults we occasionally see tubular and rounded groups of egg-cells, in which the process of subdivision into follicles by constriction is not yet completed. I have frequently seen formations of this kind, and also depressions of the superficial epithelium (see fig. 214), in Dogs, Rabbits and Birds; still it remains an open question whether these appearances are not the remains of former periods of growth; at all events I have not yet been able to persuade myself that the contrary is true: Koster's (60) statements are similar to the above.

If we glance over the results obtained, it will be seen first that the stroma of the ovary does not, either through its cellular elements or in any other way, produce the egg—a view which, before Pflüger's pioneer work, the majority of investigators had sought to prove—but that it is simply the support of a peculiar epithelial formation, which from the very beginning developed itself, as an independent embryonic deposit, entirely distinct from the stroma, and stands in the same contrast to the latter as do everywhere the products of both epithelial laminæ of the embryo to their vascular connective-tissue supports.

Certain observations in pathology, as for instance the development of numerous dermoid cysts in the ovaries, have already long since led to the search in that organ for cells belonging to the horny layer. The well-known statements of His (52) could not be verified, and since then the attempt has not been successful to obtain more accurate proof bearing on this point by the study of the process of development. I would like to call attention, however, to a work of Van Bambeke's (6), which I have only recently been able to see: this author has found that in Pelobates fuscus the outermost germinal layer, which produces the largest portion of the epidermoid elements, dips down on both sides of Ecker's vitelline plug, at Rusconi's and Remak's anal fissure, into the cavity of the egg, there to form a portion of the third germinal layer; while at the same time the cells of the remaining portion assume entirely the character of the cells belonging to this incurving part. From this third germinal plate in the Batrachia, however, are produced the internal organs of generation and the Wolffian bodies; this circumstance should perhaps show us the right track to follow in the investigation. (See Götte's (47 *a*) preliminary communications on this topic.)

A very remarkable circumstance is the early appearance of the eggs, which in all classes of animals are simply more fully developed, especially perfect epithelial cells of the ovary; hence the follicular epithelium and the egg-cells also stand in a direct genetical relation to each other.

I would call attention in this place to El. Mecznikow's (74) "pole-cells." In the Cecidomyids he found that the youngest ovarian deposit, consisting of a mass of cells, was characterized, even when it first appeared, by the presence of special cells, which he called "pole-cells;" these were the youngest eggs.

If we can consider it as settled that no new formation of eggs takes place later, then we should have in these elements one of the most remarkable

instances of longevity among elementary organisms; this is true at least in Man, where they may live fully forty years.

We have everywhere become acquainted with the accessory appendages of the primordial egg-cell, such as the subordinate yolk and the zona pellucida, as products of the follicular epithelium. Hence we can only consider the primordial egg as a simple cell, the mature ovarian eggs being already complex bodies.

This view would seem to be contradicted by the experience that the eggs of the Batrachia and of Mammals, as well as those of many of the lower animals, undergo subdivision in all their component parts. The contradiction, however, is not yet surely binding. On the one hand we may ask whether the products of the follicular epithelium, which is genetically related to the egg, cannot, when supplied in small quantity, be entirely assimilated by the primitive egg-cell. On the other hand, however, it is very doubtful whether, in the animals mentioned above, all the component parts of the egg contribute directly to the formation of the embryonic body. At least so far as the Batrachia are concerned, Götte (47) has called attention to the fact that the so-called glandular germ-material of Remak, which is considered as a product of the segmentation, serves chiefly as nourishment to the larva. In this matter we still need more accurate investigations on segmentation and the relations of its products to the cell.

At all events there seem also to be eggs with which no subordinate yolk is associated. Leaving out of the account the eggs of the Protozoa, concerning which at the present time we can form no judgment, it may be mentioned that Ganin (41) has recently found in a few of the Hymenoptera, which belong to the subdivision of Pteromalina. mature eggs without any vitelline granules, whose germinal vesicles were surrounded by only a small amount of transparent protoplasma.

The comparison of the eggs of different classes of animals becomes an easy matter after the foregoing description. The primordial eggs are everywhere alike; the mature ovarian eggs of Vertebrates are also entirely alike, inasmuch as all are composed of the primordial egg, together with a material which is always produced in the same manner by the follicular epithelium. The various and, to a certain extent, very artificial classifications into which it has been customary to divide eggs, are thus done away with in a very simple manner.

The comparison between the ovaries of the different species of animals is more difficult to carry out. In the lowest groups of animals they appear to be reduced to their simplest yet most essential element—the egg-cell; in many Worms and Cœlenterata, we find in the place of special organs a few spots in the abdominal wall which are simply covered with the germ-epithelium, but do not possess any specially arranged vascular under-layer; and the cells of the germ-epithelium by simple growth become developed into eggs. The Echinoderms, Molluscs, and by far the greatest part of the Arthropods, possess already special organs whose structure is built on the type of tubular or clustered glands. Moreover there is found in the Molluscs and most of the Arthropods that arrangement of egg-follicles which is a constant and I might almost say characteristic phenomenon in Vertebrates. At the same time the primordial egg-cell is enclosed by the formation of special accessory parts in a compartment of its own, which is completely surrounded by a vascularized stroma. The contrast which exists here between the higher Vertebrates and the lower—the Batrachia and Osseous Fishes, and also most of the Invertebrates—is specially noteworthy. In the former at least a portion of the ovarian epithelium remains exposed to view, while in the latter all the epithelium is entirely enclosed in a vascularized stroma. We must imagine this enclosing of the epithelium, in the Amphibia and Osseous Fishes, to have taken place in such a manner that the germ-epithelium —which originally in all Vertebrates was spread out over the surface—

together with the epithelium of the tube, became surrounded on all sides, as the development progressed, by a vascularized stroma. In most of the Osseous Fishes, this process takes place in direct connection with the tube, whose broadened blind termination seems here to constitute the ovary. In the higher Vertebrates this total embedding of the epithelium does not take place either in the ovary or at the ostium abdominale of the tube.

The entire plan on which the ovaries are constructed resembles closely the type of the true, that is, epithelial glands; we have here, as there, rounded or oblong masses of epithelial elements embedded in a vascularized stroma that serves as a support both for them and for the vessels; then in the liquor folliculi and subordinate yolk we have the requisite secretion.

We have finally still to account for the subsequent fate of the Graafian follicles, which play a part both in ovulation and in the formation of the yellow bodies—corpora lutea. Both processes stand in the closest relation to each other, a fact which, although formerly supposed, has only recently been proven by Spiegelberg (109).

In each mature Graafian follicle, at its most prominent portion, there is an oblong spot, free from blood and lymph vessels, called the cicatrix—the stigma or macula folliculi. At this spot the wall of the follicle ruptures to give exit to the egg. The processes which cause this rupture are of a twofold nature; in the first place, as Spiegelberg has shown, an extensive fatty degeneration takes place in the cells of the wall of the mature follicle; and then a motive power is furnished in the development of the corpora lutea, which begins already some time before the opening of the follicle. The latter process consists in an abundant growth of cells, both from the follicular epithelium and from the tunica propria folliculi; from injections made with fine particles of coloring matter I am led to believe that numerous wandering cells make their way through the latter membrane into the cavity. In addition to the wandering cells, vascular arches spring forth from the sides into the cavity of the follicle; in this way the space grows constantly narrower and is finally compelled to burst at the weakest spot in its wall, that is, where there are no vessels. Then the egg escapes, and with it, in Mammals, the liquor folliculi and Discus proligerus, which latter is still attached to the egg. Whether there is always an escape of blood at the same time seems very questionable to me, and Pflüger (84) also denies it. That the menstrual congestion must promote the rapid growth of the corpus luteum, and therefore have a direct influence on the escape of the egg, is evident from the above-mentioned manner in which the yellow body is formed.

The yellow body attains its full development, however, only a few weeks after the follicle has burst; or, where impregnation has taken place, only after two or three months. The mass of which it is formed occupies the former place of the follicle, but surpasses it in size; it consists of a central portion, which at first is somewhat red but later has a clear gray color, and of a peripheral portion, which is thrown into folds and is intensely yellow; on the outside it is invested by the former tunica fibrosa of the follicle. In the fresh corpus luteum the central portion consists of a highly vascular tissue, resembling mucous tissue, in which are usually embedded numerous large cells, filled with granules of a red coloring material and crystals of Hæmatoidine (see Zwicky, 129, and Virchow, 120). The peripheral zone consists of two kinds of cellular elements: nearest the centre there are seen large, pale, finely granular cells, with rounded angles, which, as may easily be demonstrated in the Rabbit, originate from the epithelium of the follicles; on all sides highly cellular processes, carrying vessels, project both from the periphery and from the centre between these large cells, giving rise

to the folded appearance of the yellow zone. Although at first the epithelial portion of the corpus luteum is so richly developed, still it seems later to disappear altogether; then there only remains of that voluminous body a small trace, which appears like a white cicatrix—the corpus albicans. The cause of this retrograde metamorphosis of the yellow bodies is attributed by His (52) to a wasting of the arteries, which here possess very thick walls. It is a remarkable fact that, when the uterus has become gravid, the yellow bodies, which are then distinguished as corpora lutea vera, become much more fully developed and persist up to the end of gestation, whereas the corpora lutea spuria undergo retrograde metamorphosis at the end of a few weeks. This would favor the view suggested by Pflüger (84), that the corpora lutea are intended to serve the further purpose of covering up the losses of substance caused by the emptying of the Graafian follicles.

The credit of thorough investigations on the subject of the corpora lutea is due to His (52). Nevertheless I cannot side with him in his belief—which is also shared by Kölliker and others—that the follicular epithelium does not participate in the formation of the yellow bodies, but must range myself on the side of Schrön (102), Pflüger (84), and Luschka (72), who hold that both elements of the follicular wall aid in its formation. Further historical data concerning the corpora lutea will be found in the dissertation of Zwicky (129).

Not all of the Graafian follicles—whose number in a young ovary Henle estimates at 36,000, while Sappey (see Frey, 40, pg. 534) places it at 400,000—become fully developed, nor by any means do all produce a mature egg; on the contrary, the majority of them die at various stages of their development: even the smallest specimens of follicles are sometimes found already in the commencement of decay, as I can with Pflüger (84) attest. In the larger degenerated follicles the remains of the egg will usually be found in the shape of a very thick, shining, compressed zona pellucida with scanty granular contents; the follicular wall undergoes very much the same change as in the formation of the corpus luteum, only the new formation of cells is very much smaller in quantity. Well-developed corpora lutea are only found in Mammals; although more imperfectly developed they are not wanting in any of the Vertebrates; degenerated follicles may be found in great numbers in all the classes of Vertebrates.

As I have ascertained by recent investigations in Dogs, the ovarian epithelium is absent from the external surface of fresh corpora lutea; nevertheless, at the spot where the former follicle ruptured, the epithelium dips deep down between the ovarian stroma and the periphery of the yellow body. Future investigations will have to determine whether a new formation of follicles and eggs does not perhaps take place from these epithelial depressions.

Paroarium.—The Wolffian body consists—as J. Müller (79) has already proven, and Banks (7), and Dursy (35), have recently reiterated—of two different portions; the one possesses broad canals, with flat, granular epithelium, and is connected with glomeruli; this is the primitive-kidney portion of the Wolffian body. The canaliculi of the second portion, which occupy in Man the upper part of the Wolffian body, are narrower and carry a deeper epithelium, which later is in part ciliated; in the Male these become developed into the canaliculi of the parepididymis. In the Female also they penetrate as far as to the hilus of the germ-gland, and, in many species of animals, deep into its stroma, as for example in the Dog (see fig. 213), the Cat and the Cow. They terminate here on both sides with blind extremities, and, after the Wolffian duct, with which they previously were con-

nected, has become obliterated—which usually occurs in most of the animals in question—their lumen also undergoes obliteration. The remains of these canals, that is, the remains of the sexual portion of the Wolffian body, which are found at one time outside of the ovary (the so-called Rosenmüller's organ), at another within it, as in the Dog, constitute the *paroarium*, the homologon of the epididymis of the Male. In the Human female this consists later of from 12 to 15 tubes which are embedded in the ligamentum latum, and whose nucleated connective-tissue walls are lined with a single layer of ciliated epithelium. In the Dog, the canals which lie deeply embedded in the body of the ovary do not carry cilia, but are lined with a pavement epithelium; they may truly be looked upon as homologa of the seminal canaliculi.

The remains also of the primitive-kidney portion of the Wolffian body are preserved entire in both sexes. In the Male it represents Giraldès' organ (Parepididymis, Henle (50); Paradidymis, myself (123)), while in the Female embryos it is found in the ligamentum latum, between the ovary and the tube, nearer the median line than Rosenmüller's organ, and distinctly separate from the latter. Later it becomes reduced to a mere insignificant trace, and is perhaps the source of many of those small cystic formations in which the broad ligament of the uterus abounds.

A tolerably complete statement of the earlier history and literature of the ovary and ovule will be found in A. von Haller's Elementa physiologiæ, Bernæ, 4, T. vii., viii., and in Valentin's Handbuch der Entwickelungsgeschichte, Berlin, 1835; the article of Farre, "Uterus and its appendages," Todd's Cyclopædia, Vol. v., and that of Leuckart, "Zeugung," in R. Wagner's Handwörterbuch der Physiologie, should also be consulted. Among the more recent dates it should be mentioned that in 1827 Von Baer (2) discovered the Mammalian egg. The germinal vesicle had been discovered already in 1825, by Purkyné (88), in the Bird's egg; Coste (31) discovered the germinal vesicle of the Mammalian egg in 1834, and almost at the same time it was seen in Breslau by Valentin and Bernhardt (13), and in London by Wharton Jones (see the communication of the latter to the Royal Society of London, June, 1835, reported in the London and Edinburgh Philosophical Magazine, III. Series, Vol. vii.). In 1835 R. Wagner (121, 122), having demonstrated the existence of the germinal spot, was able to draw a preliminary conclusion in regard to the morphology of the egg (see also J. Müller's Archiv, 1835, p. 373, and "Denkschriften der Bayrischen Akademie der Wissenschaften zu München, 1837, II., 531). In his Prodromus (121) Wagner also attempted to make a comparative classification of the eggs of all the known varieties of animals. A representation of the micropyle in the egg of the Holothuria is given already in R. Wagner's Icones zootomicæ; Doyère appears to have seen it already in 1850 in the Syngnathidæ (see Reichert's Jahresbericht pro 1854, and Müller's Archiv, 1855). J. Müller (80) first described it more accurately in the egg of the Holothuria, and compared it to the micropyle of Plants; then Keber (55) expressly proposed the term "micropyle" for this opening. To Valentin (116) is due the first demonstration of tubular, branching, glandular structures in the ovary, a discovery which was soon afterwards confirmed by Billroth (15); nevertheless, it received but little attention until Pflüger (84) had again confirmed the fact, and, in an excellent monograph, had given a new direction to the views relative to the structure of the ovary. We have already, so far as our space would permit, communicated in the text Pflüger's views in regard to the origin of the Graafian follicles from tubes, the development of the eggs, their structure, their constant new formation, even in the adult, and the peculiarities of the ovarian epithelium. Before then it had always been customary to consider the follicles and the eggs as the offspring of the ordinary stroma-cells of the ovary; subsequent to Pflüger, however, histologists learned to look upon both as independent epithelial formations, which were simply embedded in the stroma. Of course the actual proof of their first development continued still to remain, it is true, a desideratum.

Pflüger's work called into existence a large number of essays on the ovary. The tubular formations were also soon discovered in the Human being, first by Spiegelberg (107), then by Letzerich (65), and Langhans (64); in the Chicken they were found by Stricker (114) and many others, and recently in Mammals by Plihal (87).

In opposition somewhat to Pflüger, who laid the entire stress on the formation of tubules, are the works of Borsenkow (22), Bischoff (19), Henle (50), Grohe (49), and recently His (52), who investigated chiefly embryonic ovaries, and first specially pointed out their cavernous structure and the rounded masses of epithelial cells in which the eggs were embedded; the same is true of Kölliker's (59) work. We must also mention here the dissertation of Bornhaupt (21), who first described the development of Pflüger's tubes in the Chicken from the ovarian epithelium. Concerning the description, given in the text, of the ovarian epithelium, and of the manner in which the follicles and eggs are developed from it, the reader is referred to the essay mentioned under No. 123 of the accompanying bibliographical list: materially the same results were obtained by Koster (60) in the researches made by him at the same time.

In order that the dimensions of the most important portions of the ovary may be seen at a glance, I have placed them together in a small table; they are compiled from the statements of Henle, Kölliker, Frey, Von La Valette, and also from my own measurements, and have reference chiefly to the Human ovary. The numbers indicate micromillimetres.

Epithelium of the surface of the ovary	(newborn Child).	Length....	15–18.
" " "	"	Breadth...	5–6
" " "	(adult Human).	Length....	12–15.
" " "	"	Breadth....	5–6.
" " "	(old Cow).	Length....	9–12.
" " "	(Calf).	"	12–15.
" " "	(Pig).	"	15–20.

		Diam. of transverse section.
Primordial follicle	(7 months Human embryo)	30–100.
Smallest follicle	(adult Human)	30–40.
Mature follicle	" "	10,000–12,000. (10–12 mm.)
Smallest follicle of the Hen		24–36.
Follicular epithelium	(adult Human)	15–22.
" "	(Hen, in follicles 3–6 mm. in diam).	24–30.
" "	(Hen, in mature follicles)	6–8.
Primordial egg	(3 months Human embryo)	11–14.
" "	(7 months Human embryo)	15–25.
Smallest eggs	(adult Human)	26.
Mature egg	(Human)	200.
" "	(Dog)	180.
" "	(Guinea Pig)	120.
Human zona pellucida	(mature egg)	10.
Germinal vesicle	(3 months Human embryo)	9–11.
" "	(7 months Human embryo)	10–14.
" "	(mature Human egg)	45.
Germinal spot	(3 months Human embryo)	2.
" "	(mature Human egg)	7.
" "	(almost mature Sheep's embryos)	5–8.
" "	(in Kittens, 17 days old)	3–5.

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CHAPTER XXVI.

SKIN, HAIR, AND NAILS.

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A. Skin.

The skin, or common integument, covers the exterior of the body, and, while serving to protect it from injuries, has other no less important functions to perform. To fulfil these it is provided with various glandular, horny and nervous elements, which are not, however, distributed equally over the entire surface, but are more abundant in certain regions; we must, therefore, consider separately the essential constituents of the whole skin and those which are peculiar to certain regions.

To the former belong the true skin, corium, cutis or derma, with its epidermal covering or cuticle, and the subcutaneous cellular tissue or tela subcutanea; the latter elements are the hairs and nails, the glands and nerve termini, which will each be studied separately.

The outer integument consists of the cutis, and the subcutaneous cellular tissue; the cutis, again, is divided into the corium or derma and the epidermis. The most important part of the skin is the corium, a white, dense, opaque, slightly elastic connective-tissue membrane. At its under surface it merges, without any very sharply defined boundary-line, into the tela subcutanea, which is likewise composed of connective tissue, but differs from the corium in its loose, succulent texture, whose interstices are, in most places, filled with fat.

Over the corium is spread the epidermis, which is soft and of a transparent gray color in its deeper strata, and whitish, hard and horny externally. It may be separated from the corium by maceration, and is found detached in certain morbid processes, also in putrefaction.

The corium is united to the deeper structures, as the fasciæ and bones, by means of the subcutaneous tissue. This connection is more or less loose, according to the tensity of the tela subcutanea and the quantity of its fat. In those portions of the body where great mobility is desired, the skin is loosely attached, and in these places the subcutaneous tissue is deficient in fat, as on the eyelids and penis, or where it lies in folds, as on the extensor surfaces of the joints.

The surface of the corium, in its normal state, is not even, but presents prominences of greater or less height with corresponding depressions; there are, furthermore, true folds or duplicatures, which may, however, be obliterated by traction as well as by distention from below in the way of subcutaneous exudation, or from superabundance of adipose matter. The slighter eminences on the skin take the form of ridges and papillæ. The former are especially marked on the palm of the hand and sole of the foot, likewise on the flexures of the fingers and toes, where they are curvilinear.

The smaller projections are called papillæ, and give a reticulated appearance to the surface of the corium, which, moreover, presents numerous furrows and excavations either between the folds and ridges, or existing independently, as on the flexures of the extremities; these are most expressed in the palms and soles. We find further certain funnel-shaped openings, the pores of the skin, which are the orifices of the sweat and sebaceous glands and the hair follicles.

SUBCUTANEOUS CELLULAR TISSUE.—The subcutaneous cellular tissue, *tela subcutanea*, consists of bundles of connective tissue from the superficial fasciæ, which advance obliquely to the under surface of the derma. These bands interweave with each other, leaving large interstices which are in turn traversed by more delicate fibres, producing still smaller spaces. The filaments themselves are for the greater part cylindrical, and in most places present irregularities similar to those in the arachnoid, and consist of a mass of wavy connective-tissue elements with numerous spindle-shaped cells between them. The tela subcutanea in some situations, as the eyelids, penis, ears, and scrotum, is devoid of fat, and in other locations encloses globules of adipose matter in its meshes in varying quantity. Thus provided with fat, it constitutes the so-called *panniculus adiposus*. The fatty particles are sometimes oval, more often polyhedral, from pressure, with a fine capillary network running between them. The adipose cells have delicate walls, and each contains a drop of oil, which is fluid during life but stiffens after death; the membrane is so distended by its contents that it is hardly ever seen in a fresh condition, but may be rendered visible after extracting the fat by means of absolute alcohol and turpentine. It is then seen collapsed, fine, and transparent, in most cases enclosing a round nucleus; sometimes we find remnants of a granular substance (protoplasm), which is most abundant around the nucleus. In some cases the fat takes the form of clustered crystals; this occurs especially in spirituous preparations.

Where there is no fat, the secondary spaces before described are traversed by bundles of connective tissue, and often by single fibrillæ, embracing between them interstices, generally triangular, filled with a serous liquid; as may be seen in preparations hardened in chromic acid.

The spaces between the single bands and fibrillæ vary in different persons and under different circumstances, depending on the amount of fluid in the individual; in pathological conditions, as œdema of the skin, they may become very great. Between the connective-tissue bundles there are often spindle-shaped cells, as is shown excellently in cutaneous œdema, where we find cells and fibres running isolated for a distance through the serous fluid which are seen to consist of granular protoplasmic masses and to have very long filiform processes, generally two, at opposite ends, but occasionally several, which for a distance appear to consist of the same granular substance, but at a greater remove from the cell have the smooth, homogeneous appearance of connective-tissue fibrillæ; these prolongations may be further traced into connective-tissue bundles. We may therefore conclude that the connective-tissue cells pass over into fibrillæ, as KUSNETZOFF found them to do in the embryo.

Besides these lengthened connective-tissue cells there are other fusiform and round cells, resembling the white corpuscles of the blood in size and appearance, only larger, with a very granular protoplasm in which a round or elliptical nucleus may be recognized, although with difficulty. The small round cells are most abundant in the vicinity of the blood-vessels. But we see numerous transition forms between the small round cells, and the larger

ones with prolongations, and that both in regard to the size of the cells themselves and the lengths of their offshoots.

Little is yet known as to the development of the adipose cells; their relation to the capillaries is, however, worthy of consideration. Nearly every fat-cell is surrounded by a vascular network; an arterial and venous twig coming to the portion of the cellular tissue corresponding to each fat globule, forming a minute capillary inosculation.

Larger blood-vessels reach the corium from the subcutaneous cellular tissue, and branches are given off from them to the adipose cells, hair-follicles, and sweat-glands; there are also nervous trunks with Pacinian corpuscles in places, and finally lymphatics, which are entirely independent of the blood-vessels. The larger lymph vessels, which show a markedly transverse muscular structure, have their own blood-vessels, the *vasa vasorum lymphaticorum*, two minute trunks accompanying each lymphatic and forming a dense network around it by their frequent anastomoses. This explains the appearance of the sharply-defined red cords in the skin in *lymphangöitis subcutanea*, they being the lymphatic ducts whose course is thus plainly recognizable.

CORIUM.—The corium likewise is composed of connective-tissue elements with an elastic meshwork, also of anastomosing connective-tissue cells, interwoven between its fibres. The fibrous bands of the subcutaneous cellular tissue are composed of fibrillæ, and at the under margin of the corium they separate into smaller bundles which run obliquely to its surface, continually subdividing into smaller fasciculi. Within the corium these fibres are interwoven with others which meet them at right angles, and a thick fibrous network is thus formed with very small interstices, which are not visible in that which has been tanned or hardened in alcohol, but are large in the succulent skin of young persons, and of greatest size in those pathological conditions which are attended with exudation into the corium; in these states, especially, it is evident that the fibrillæ include rhomboidal spaces.

This symmetric texture of the corium is disturbed in those places where various structures penetrate the skin in a perpendicular or oblique direction, as the hairs, sweat-glands, and their ducts, blood-vessels and nerves, inasmuch as these are accompanied by their own proper connective-tissue sheaths of variable thickness.

As before stated, the coarse connective-tissue bands which enter the corium break up into smaller fibres and finally into separate fibrillæ. In the deeper portion of the corium the distinct bands interlace, giving this part a reticulated appearance, whence the term *pars reticularis corii* in contradistinction from the upper portion, the *pars papillaris*, in which the single fibrillæ alone decussate. There is, however, no sharply defined boundary-line between these two, nor between the corium and the subcutaneous tissue, where the latter is wanting in fat.

The outer surface of the corium presents numerous wart-like prominences, the *papillæ*, which vary in height and breadth in different places, sometimes being shaggy or filiform, as on the fingers, sometimes forming little tuberosities, as on the larger part of the body. The regular arrangement of the fibrillæ is disturbed by these elevations, the fibres which run parallel to the surface being bent into loops within the papillæ. The natural course, however, of these most superficial fibres is not entirely straight, but somewhat wavy, so that the whole surface of the corium as well as the papillæ is not quite even. The perpendicular fibres of the corium also pass into the pa-

pillæ, for the most part accompanying the capillaries, and probably terminate within the papillæ in free extremities.

The surface of the corium is everywhere covered by a delicate cuticula, which is most clearly visible in chloride of gold preparations. Between the rete Malpighii, which is stained red or blue in these specimens and the

Fig. 221.

Fig. 221. Preparation in chromic acid. *a*, vascular papilla; *b*, nerve papilla; *c*, blood-vessel; *d*, medullated nerve fibre with a thick nucleated sheath; *e*, sensation corpuscle; *f*, transverse section of medullated nerve fibres.

similarly colored corium, a thin, crystalline membrane is seen uncolored, in which oval cells are imbedded here and there, parallel to the surface of the derma. This membrane is not sharply defined toward the corium, but more so on the side of the mucous layer, which, besides showing slight depressions, is finely dentate in many cases. Exteriorly it presents delicate ribs or even filiform projections which interlace with similar ones of the mucous cells. According to Czerny, it presents tracings after treatment with nitrate of silver similar to those on the lymphatic walls.

The elastic fibres are an important constituent of the corium, and in its deeper portions form a coarse network, which becomes more dense as it approaches the surface; they are recognized by their sharp contour and undulatory course, after saturating the connective tissue with acetic acid.

Besides the elastic and connective-tissue fibres there are also cells in the corium, which are either spindle-shaped and lie within the connective-tissue bands or which anastomose freely between them in the deeper portions and between the fibres above. There are also fusiform cells between the connective-tissue fibres which envelope the blood-vessels and capillaries; likewise round or oval cells, resembling the white blood corpuscles in size and form, mostly in the neighborhood of the blood-vessels, or sometimes even far removed from them. Their number and size vary in different persons and appear to depend on the succulence of the skin. In the young

their quantity and size is not less than in the cornea itself, whose cells they much resemble after being treated with chloride of gold.

The cutaneous *papillæ* are divided into vascular and nervous. Medullated nerve fibres constantly enter the latter, bearing the bodies called by Meissner tactile corpuscles; the former contain capillary loops. The dimensions and number of the cutaneons papillæ vary in different portions of the skin. They are most developed on the inside of the hand and fingers, where they form rounded cones with circular bases and are arranged in double rows upon the ridges before alluded to. In these places they attain a length of 0.1 to 0.2 millim. and almost touch each other at their bases, or stand slightly separated, while on other portions of the skin they are hardly half this height and represent only hilly elevations of the dermal surface. Often their bases unite, forming the compound papillæ.

Not less variable is the whole thickness of the corium, not only on different parts of the body, but also on different persons of the same race. According to Krause, the thickness of the corium, which, on account of its gradual transition into the subcutaneous tissue, can only be approximated, amounts on the eyelids and prepuce to 0.56 millim., on the glans to 0.27 mm., on the face, penis, and areola of the breasts from 0.76 to 1.12 mm., on the forehead 1.52 mm., on most other parts 1.69 to 2.25 mm., on the back, sole of the foot, and palm of the hand from 2.25 to 28 millim.

Blood-Vessels of the Corium.—The vascular trunks which ascend obliquely through the subcutaneous tissue and give off branches there to the fatty tissue, sweat-glands, etc., anastomose freely in the deeper parts of the corium, forming a network from which twigs run in a slanting direction to the outer portion. In the external strata of the corium, at the boundary between the pars reticularis and papillaris, we find a second vascular plexus with finer meshes which correspond more or less to the bases of the papillæ. From this vascular loops enter the papillæ and for the larger part occupy their centre as far as their summit. But every papilla does not possess a capillary; those generally remain unvascular in which the medullated nerve fibres enter, although there are many exceptions to this rule.

Lymphatics of the Skin.—The lymph-vessels proper must be distinguished from the lymph spaces of the skin. The former are definite canals bounded by their own proper walls; the latter, on the other hand, are interstices in the tissue of the skin between the blood and lymphatic vessels, which are filled with a serous fluid. The lymphatic trunks of the subcutaneous cellular tissue have muscular coats; they anastomose abundantly and run obliquely to the under surface of the corium, where they form a double network, one over the other, in a manner similar to that of the blood-vessels (Teichmann, Young).

In the outer portion of the corium this lymphatic reticulation lies beneath the already described vascular plexus and encloses polygonal spaces by its minute inosculations (0.018 to 0.054 millim., according to Teichmann). The deeper network lies under the lower capillary plexus, and consists of greater tubes with meshes larger than the preceding. These two lymphatic webs are connected by a few quite sizable vessels running obliquely from one to the other. In a normal condition the papillæ contain no lymphatics, but on the sole of the foot, where they are hypertrophied, branches with blind extremities penetrate the papillæ to one-half their length (Teichmann).

The walls of the lymphatics of the outer portions of the corium present a

tessellated appearance rendered visible by a silver discoloration, while in those of the deeper portions a delicate network of elastic fibres is superadded.

When describing the corium we mentioned the existence of interstices between its fibres which are filled with a serous fluid varying in quantity with the condition of the individual. In pathological states, as in acute and chronic exudations, for example œdema, these spaces are for the most part the seat of the effusion. They have no definite walls of their own, and the œdematous fluid is emptied from a comparatively large space by a superficial incision. These interstices are designated lymph spaces, although no direct connection can be demonstrated between them and the lymphatics proper.

The relation between the lymph and blood vessels is worthy of note. Although both the course and arrangement of the large lymphatic trunks are independent of those of the blood-vessels, still we frequently find a state of things, especially in œdematous skin, which bespeaks a certain relation between these two varieties of vessels. Thus, the lymphatics for a long distance are accompanied by a capillary, sometimes by two, and these touch their walls and often encroach upon the cavity to the extent of half its diameter. According to Langer the larger cutaneous blood-vessels of the Frog are attended with two lymphatics, while in the subcutaneous cellular tissue of Man the relation is so far reversed in many places, as the penis and extremities, that the larger lymph ducts have two accompanying blood-vessels which anastomose freely around them by means of capillaries. Many, including Stricker, have described *perivascular lymphatics* which others, with Langer, have denied.

The lymphatics of the Human skin have special epithelial walls, the blood-vessels not. We have already mentioned that the blood-vessels, even the capillaries, are surrounded by parallel connective-tissue fibres, with fusiform connective cells; between these and the wall of the vessel, as in other tissues, we find the interstices alluded to containing serum, whose size varies, and which may be rightly called lymphatic spaces.

Epidermis.—In perpendicular section the corium is seen to be covered externally with a membrane which is designated *epidermis* in the broadest sense of the word, and which Malpighi divided into two layers, an outer, the true epidermis, and an inner, the mucous layer, stratum mucosum, rete or mucus Malpighii. The latter consists of epithelial cells filling nearly all the depressions in the surface of the corium, and therefore presenting elevations and depressions on its under surface corresponding to those of the surface of the cutis; the former, however, is composed of epidermal scales arranged in lamellæ with a stratified or fibrillated appearance on cross section.

Mucous Layer.—The cells of the first row adjoining the corium are small, 0.006 millim. in diameter, with oval nuclei; they are for the most part cylindrical, with their axes perpendicular to the surface of the derma. They consist of a slightly granular lustrous protoplasm surrounding the compact nucleus and having no cell wall. Sometimes, as, for instance, in new-born Children, the outlines of the individual cells of this layer are obliterated so that the surface of the corium is covered with a protoplasmic mass having nuclei scattered regularly through it (Henle).

The cells of the next row are cubiform, and are larger than those in the first layer; they have a sharper outline and an oval nucleus slightly granular, within which two nucleoli are frequently found; the surface of this

stratum in most cases presents slight dentations. The cells of the next three strata are larger, they assume a polygonal shape and enclose a round nucleus, or occasionally several. Their cell body is homogeneous, and a surrounding membrane is clearly visible which in most places sends out prolongations or serrations which are attached to the neighboring cells (ribbed or stellate cells, Max Schultze). The nearer the external surface of the mucous layer we approach the more the cells flatten, so that their long axes are finally parallel to the surface of the skin; the body of the cell becomes more hard and symmetrical, the nucleus smaller and often surrounded by a slight areola. This is readily seen on section in a preparation hardened in chromic acid, where a round empty space appears within the cell; but more frequently in the cells of this row we find the vacant spaces circular, and resembling cell nuclei in size, on one side of which lies a semi-lunar shrunken flat nucleus. There are small vacuoles within the cells, especially in the more superficial ones of the mucous layer, which in a fresh condition are probably filled with a clear fluid.

But besides these cells which have an epithelial character we find others of a different kind scattered here and there in the rete Malpighii, exsected from living subjects. These are most readily recognized in the outer and middle strata of the rete, mostly by the lustre of their protoplasm and by their small size. They are generally extended in length, being compressed between epithelial cells, or they send delicate prolongations between the cells of the epithelium. Their protaplasm is very clear and is brilliantly stained by carmine; the small nucleus, which is with difficulty recognized, may as a rule be discovered after the imbibition of carmine. These cells are still more difficult to recognize in the deeper layers of the rete Malpighii, for they closely resemble the cells of the latter, whose protoplasm is likewise shiny and becomes deeply dyed in carmine, so that they are distinguished from those in question only by their well-marked nucleus. They are most readily recognized when they lie one-half between the cells of the rete Malpighii and the other half still in the corium (Biesiadecki). These cells remind one strongly of the so-called migrating or wandering cells which are found in the subcutaneous connective tissue, especially in the neighborhood of blood-vessels, and also between the fibrillæ of the corium, and further, in the mucous layer; they occur in small quantity in the healthy skin, but in larger numbers in pathological states (Condylomata acuminata, and Eczema. Biesiadecki).

The rete Malpighii is best studied on skin which has been hardened in chromic acid or Müller's fluid; spirituous preparations are of little value. The migrating cells above described are found only in very rare cases in sections from the cadaver. They are more apt to be seen in young persons, in parts with a thick mucous layer; and are most readily traced on skin which has been irritated by blisters, or over inflamed papules, also in œdematous skin. The facts that we find these cells half in the corium and afterwards in the various strata of the rete Malpighii in all possible forms, that their number is augmented in irritated skin, and that they are but sparingly present in the normal condition, all speak in favor of their individual locomotion, just as cells have been observed to change their place in other structures with like peculiarities.

The cells of the mucous layer are with difficulty separated from each other either by mechanical means or by chemical agencies. This intimate union between the different cells is due perhaps not so much to any connective material as to the interlacing of their prolongations and ribs. They are most readily isolated from each other by boiling portions of skin which have

been hardened in chromic acid in a tolerably concentrated potash solution for a long time; the mucous layer thus separates in a mass from the corium, and the epidermal cells after a little while fall apart on slight agitation with a glass rod.

HORNY LAYER, STRATUM CORNEUM.—The cuticle or epidermal layer appears on cross section to be fibrillated, with its fibres running a somewhat undulatory course parallel to the surface of the skin. Even higher magnifying powers give no nearer insight into its structure, which is only learned after separation of the apparent fibres. We then find that they consist of a mass of flat polygonal scales, the so-called epidermal or horn cells.

In the deeper strata adjoining the mucous layer these cells are somewhat larger and resemble those of the latter, only they are somewhat flatter, less granular, and are not stained by carmine, while in most of them the nucleus has entirely disappeared; a few have a slightly oval nucleus, likewise flat, having, on the average, a diameter of 0.005 to 0.008 millim. The scales of the outer layer are flat, polymorphous and curved; they have a sharply defined and simple outline, are without nuclei, and of a transparent lustre. They swell in water to some extent, become opaque, dark and granular, and in acetic acid or caustic potash they expand to vesicles, within which there are delicate filaments or nuclei, or a wrinkled structure resembling a nucleus may be visible in the centre. The division of the horny layer into lamellæ results from the firm adherence of its cells, and this gives it the fibrous structure on cross section. Inasmuch as the rete Malpighii does not completely fill all the depressions in the surface of the corium, small eminences are formed over the projections of the corium, or papillæ, with corresponding depressions in the surface of the rete mucosum. The laminated horny layer follows these inequalities, giving the wavy direction to the single scales. But the epidermis follows in like manner the deeper irregularities of the corium, as for example the ridges and furrows on the palm of the hand, giving to it its well-known appearance.

The thickness of the epidermis varies considerably in different persons and different parts of the body. Often the horny layer forms a thin covering over a greatly developed rete Malpighii, while in many places the former is twice or three times the thickness of the mucous layer. But in both instances the latter preserves in general a uniform thickness, with the exception of those places where the papillæ are long, between which the mucous layer has considerable thickness, while over the papillæ it is proportionately thin.

According to Krause the rete Malpighii varies from $\frac{1}{65}'''$ to $\frac{1}{20}'''$, while the horny layer on the other hand ranges between $\frac{1}{65}'''$ and $1'''$. Both together often measure 3.7 millim., but in most places not more than 0.05 to 0.25 millim.

The dark hue which in some persons is found over the whole skin and in others only in certain places, as on the areolæ of the breast, scrotum, etc., depends upon the presence of coloring matter in the cells of the rete Malpighii. In these places there is a fine, granular, brownish yellow pigment in the deepest cells of the rete mucosum, which is in small quantity in the lighter complexioned and more abundant in those of darker tint. In the next layer externally we find fewer pigmentary granules and a more uniform light yellow staining of the protoplasma, which diminishes as we near the surface, so that, in the scales of the epidermis, the color can be determined only by comparison with those which are colorless. The dark hue of the negro depends likewise on the pigmentary contents of the mucous layer. In patho-

logical states the above-described migrating cells also contain pigment (Biesiadecki in Condylomata acuminata).

Nerves of the Skin.—Until quite recently we were acquainted only with the medullated nerves of the skin and their terminations, the *Pacinian corpuscles* and those of *Meissner*. Later investigations have further revealed an abundant plexus of nerves wanting a medulla, and terminating in free extremities between the cells of the rete mucosum.

The subcutaneous nerve trunks divide at the under surface of the corium into several branches which accompany the blood-vessels, and consist both of medullated fibres, and those without a medulla. The nerves of those portions of the skin which have a larger number of palpation and Pacinian corpuscles are richer in medullated fibres (Langerhans *).

In the subcutaneous tissue or in the deeper portion of the corium the individual medullated nerve fibres are given off from the nerve branches and terminate within the corium in the so-called Pacinian corpuscles. The rest of the nerves ascend, mostly in an oblique direction, to the surface of the corium, and form a nerve plexus in the stratum papillare corii corresponding to the vascular network.

Single nerve fibres often lose their medullary portion in the upper part of the corium, or they enter the nerve papillæ and end in the palpation corpuscles. The non-medullated accompany the capillaries into the vascular papillæ (Langerhans).

Pacinian Corpuscles.—These were discovered by A. Vater, as Langer has shown, and were called from him Vater's corpuscles. Besides being found in Man, they are frequent in many Mammalia and Birds, mostly in the subcutaneous tissue, but also in other places, as in the mesentery of the Cat. They are nothing more than the considerably thickened ends of medullated nerve fibres.

Their immediate sheath consists of a homogeneous nucleated membrane on which an epithelioid tracing can be produced by nitrate of silver. In a certain circumscribed portion it subdivides into a laminated arrangement of enveloping capsules, from twenty to sixty of which make the mass of the corpuscle. These are transparent, apparently structureless membranes, the outer of which are thicker and more separated from each other than the inner, which lie very close together. On cross section we find numerous oblong nuclei in them which are rendered more distinct by the action of acetic acid, and are stained red in chloride of gold. Seen from the surface these membranes, both in their fresh condition and after being treated with various reagents, form a somewhat punctate, uniform mass with an indistinct striation; a silver solution develops a reticulated appearance in them resembling the lymphatics (Hoyer †). The tracings are commonly irregularly pentagonal, surrounded by wavy dark-brown outlines within which lie the above-mentioned nuclei.

The medullated nerve fibres enter these independent laminated structures with spiral twistings and occupy the cavity of the innermost capsule. The axis cylinder now runs in the interior to the blind extremity and terminates there in one or several small tuberosities. The nerve medulla on the other hand fills the cavity of the inmost capsule (Innenkolben, Kölliker) and forms a finely granular or coarser mass which is but little lustrous compared to the

* Virch. *Arch.*, Bd. 44, 2d and 3d Heft.

† Archiv von Reichert und Du Bois, 1864, 1865.

white substance, but which like it becomes of an intense violet hue by means of chloride of gold.

A large blood-vessel enters near the nerve fibre and forms an abundant capillary network between the outer capsules.

The Pacinian or Vater's corpuscles in Man measure from 1.1 to 4.5 millim. and are uniformly found on the cutaneous nerves of the fingers and toes, on the palms and soles, also in the flexures of the joints (Raeuber). They are occasionally found on the superficial nerves of other parts and in the great sympathetic plexus behind the peritonæum near the abdominal aorta, also near the fundament.

MEISSNER'S OR WAGNER'S CORPUSCLES, PALPATION CORPUSCLES.—The medullated nerve filaments, which run beneath the papillæ with the blood-vessels, here and there ascend into single papillæ, which as a rule are non-vascular, and terminate in the so-called tactile corpuscles—*corpuscula tactus*—of Meissner and Wagner.

If we harden the skin of the last phalanx in chromic acid, in some of the low broad papillæ we find oval bodies which occupy their entire length and have a diameter of from 0.02 to 0.045 millim. These (fig. 221) attract attention by their firm appearance and transverse striation, which is produced partly by fine lines and partly by fusiform lustrous cells placed diagonally. The medullated nerve fibres, with their nucleated sheaths, run sometimes only to the lower extremity, sometimes to the middle or even to the summit of the corpuscle, and are often wound once or once and a half time around the corpuscle, which is then narrowed at that portion. Suddenly they lose their medulla and can no longer be traced in the corpuscle.

Similar appearances are seen after treating fresh sections of skin with potash, soda, or concentrated acetic acid. There are many questions about them which are yet undecided, and have been answered in various ways by different observers. The transverse lines by some are thought to be connective tissue, by others elastic tissue or nerve fibres, and the corresponding nuclei have been taken for connective-tissue cells or nuclei of the nerve sheaths. Some have supposed that the nerves after losing their medulla entered the cavity of the tactile corpuscle, after the manner of Krause's corpuscles, and ended there in free extremities.

We have been able to settle several disputed points by means of successful chloride of gold preparations, the nerve fibres being colored of a dark violet hue, while the rest of the tissue has a pale reddish color; the contour of the corpuscles is visible in a faint outline within which lie the oblong nuclei. Delicate sections reveal the existence of from four to six violet nerve fibres within the corpuscle, sometimes obliquely directed, sometimes longitudinally, which are accompanied with small nuclei but little colored. Thin sections, however, give no explanation as to their further course; they do not show whether the fibres subdivide or how they terminate. The corpuscles of Meissner, as also those of Pacini, are the terminal structures of the medullated nerves, but we are not acquainted with the manner in which they end within them.

Tactile corpuscles are always found on the last phalanges of the fingers and are most numerous here. According to Meissner * there are in this situation 108 tactile to 400 vascular papillæ. They are found in less quantity on the palm of the hand and sole of the foot, as well as on their dorsal surfaces, and also in the nipples, though not always (Kölliker, Krause), and in the lips (Kölliker, Krause, Henle).

* *Beiträge zur Anatomie und Physiologie der Haut.* Leipzig, 1863.

TERMINATIONS OF THE NON-MEDULLATED NERVE FIBRES.—In the pars reticularis corii, along the ramifications of the capillaries, the non-medullated fibres form a plexus which consists partly of coarse fibres and also of others fine, smooth and varicose, with numerous nuclei. From this plexus single nerve fibres ascend towards the rete mucosum, which sometimes run first for a distance beneath it, and then, turning suddenly, enter the mucous layer. Others reach the papillæ, subdivide within it, and mount between the cells of the rete Malpighii (Langerhans, Biesiadecki). This disposition can be traced only on preparations which have been successfully treated with chloride of gold, and these are very difficult to obtain, the most frequent obstacle being that the saturation of the corium is imperfect, owing to the impermeability of the horny layer. Langerhans therefore recommends placing only thin sections of cutis in the solution of chloride of gold, to which a few drops of acetic acid have been added.

In favorable specimens by this method the nerve fibres are readily seen entering the mucous layer and ending there in knob-like distentions, at the height, perhaps, of the third row of cells. Also in the more external layers of the rete Langerhans asserts that he has seen a considerable number of deep violet-colored bodies, each of which sends a prolongation downwards and several outwards towards the stratum corneum. He thinks the former are connected with the deeper nerve fibres.

SEBACEOUS GLANDS.—The sebaceous glands, *glandulæ seboferæ*, called also the glands of the hair follicles, on account of their connection with the hairs, are simple or compound acinous glands whose ducts, as a rule, open into the hair sac, and seldom directly on the surface of the skin. In the case of the larger hairs they form appendages to the hair follicle, while with the downy hairs the relations are so reversed that the small hair seems to lie within the broad duct of the gland. They are always situated in the corium, and never extend into the subcutaneous connective tissue.

The sebaceous glands consist of a body and duct. The body of the gland is in lobes (acini), that is, pear-shaped sacs filled with enchymatous cells, from two to twenty of which have a common orifice. The acini consist then of a glandular sac or covering, and enchymatous cells.

The sac is a transparent membrane with nuclei and apparently structureless, but showing groups of cells after treatment with a solution of silver; externally, however, there is a thick membrane formed of connective tissue and elastic fibres, in which there is a moderately developed vascular network. Neither lymphatics nor nerves have ever been recognized in connection with the sebaceous glands.

The enchymatous cells fill the whole sac with the exception of a small central cavity, and are epithelial in character, of which the more external resemble the deeper cells of the mucous layer, only the nucleus is more clearly discernible. Internally the cells first become filled with small fatty granules, and then with larger drops of oil, which obscure the nucleus and even distend the cell. After extraction of the fat we find round spaces of various sizes corresponding to the drops of oily matter within the polygonal sharply-defined cells, and these are surrounded by the remnants of the protoplasm. In the centre of the cell lies the round vesicular-like nucleus. In many instances even the peripheral gland cells are filled with fat, while in other cases the oily contents are very insignificant. In the cavity of the sebaceous gland we find a shapeless mass of sebum with abundant residue of cells.

The glandular sac passes over into the wall of the duct, which again is

continued into that of the hair follicle, so that the former is to be considered as a diverticulum of the hair sac, which is more evident from the fact that the root-sheaths also surround the orifice of the gland and pass over immediately into its enchymatous cells. The tunicle of the duct consists likewise of a pellucid membrane with an epithelial coating, enclosing a cylindrical canal generally filled with fatty matter. The cells correspond exactly to those of the outer root-sheath of the hair, and are covered with a horny layer which decreases in thickness towards the gland.

The number and size of the sebaceous glands does not depend upon the size of the hair. The bodies of the glands attached to the larger hairs consist of numerous lobes which surround the middle third of the follicle crescentically, separated only by a slight amount of connective tissue. Their size depends on the one hand on the number of the lobes, and on the other, on the quantity of enchymatous cells and their richness in fat.

The ducts of the sebaceous glands, of which one or two enter one follicle, open into the latter at an acute angle, their cells finally uniting with those of the outer root-sheath. The acini of the glands belonging to the downy hairs on some places are larger and more numerous than others, and the duct exceeds that of the other hairs.

No sebaceous glands are found on the palm of the hand, sole of the foot, back of the third phalanges, or glans penis.

The sebiferous glands begin to be developed in the third month by the formation of a small excrescence from the outer root-sheath at the height of the future gland. It is composed of epithelial cells which afterward increase in number and form a pear-shaped prolongation from the follicle.

Sweat Glands.—The perspiratory glands, *glandulæ sudoriferæ*, are convoluted tubular structures which open on the surface of the skin by a lengthened duct. They may be divided into the body of the gland and its outlet.

The body or coil is a small roundish yellow knot which is almost always situated in the subcutaneous cellular tissue, rarely in the deeper part of the corium, and measures generally from 0.15 to 0.5 millim. In the axillæ they attain the size of from one to two millimetres or even five millimetres in diameter.

This coil is formed of the glandular tube, wound up many times and held in position by loose connective tissue. The blind extremity lies in the centre of the coil, which may be unravelled with comparative ease, and has been known in one case to measure three-quarters of a line (Krause).

The glandular tube consists of an enveloping sheath and enchymatous cells. The sheath is formed of a thin transparent membrane, which, on the application of a nitrate of silver solution, assumes a mosaic-like tessellation (Czerny) with oblong nuclei. The loose connective tissue between the convolutions of the coil consists of delicate fibres running parallel to the glandular canal, between which are fusiform connective-tissue cells. This connective tissue forms a sort of capsule around the gland and encloses a vascular network in its fine meshes. In the larger glands, as those of the axillæ, there are numerous muscular cells, longitudinally directed, outside the membrane.

The cavity is lined with a single row of conical or cylindrical cells.

Inasmuch as the coil lies in the subcutaneous tissue, the duct of the sweat gland must traverse the whole corium, as also the mucous and horny layers of the epidermis. In the corium it has a straight or slightly wavy course, and, emerging between two papillæ, it passes with slight undulations through

the mucous layer which is there the thickest. As the cubic cells of the rete Malpighii become flattened externally, the duct of the gland must be tortuous in proportion to the thickness of the former. Where the horny stratum is thin the canal describes hardly half a turn, but when it is very thick there may be as many as twenty, resembling a corkscrew, which are always direct-

Fig. 222.

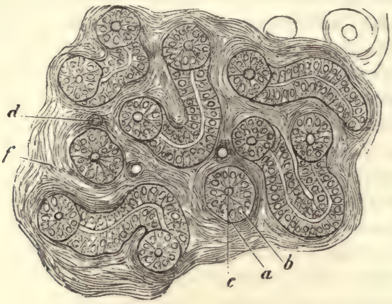

Fig. 222. Coil of a Sudoriferous gland, cut in many directions. *a*, external membrane; *b*, enchymatous cells; *c*, glandular canal; *d*, divided blood-vessel; *f*, loose cellular capsule.

ed towards the right, on both halves of the body (Welcker). In some places, as the hands and feet, the orifices are conically dilated and are visible to the naked eye as the so-called *sweat-pores.* In the last-mentioned situations they are arranged in rows in the furrows, at equal distances from one another, elsewhere mostly in groups (Krause). They do not exist on the prepuce and glans penis.

In the mucous layer the ducts have no enveloping membrane of their own, the canal being surrounded by the concentric concavo-convex cells of the rete and by scales in the horny layer.

The ducts form tongue-like projections of the mucous layer into the corium and, on macerated skin, they may be drawn out with the epidermis as fine threads. Here in the derma they possess a separate membrane of their own which is to be considered as a continuation of that covering the corium. The mucous layer is continued into the cavity of the gland in multiple rows of cells, decreasing gradually in thickness till finally, deep in the corium, they pass over into the enchymatous cells. Connective-tissue fibres with numerous cells accompany the duct, running parallel to it through the coras a rule also two small blood-vessels.

Langerhans (l. c.) describes between the cells of the outer portion of the duct structures belonging to the nervous system and resembling those that ium, and exist in the mucous layer.

According to Krause's reckoning there are 2,736 sweat glands on a square inch of skin from the vola manus, on the sole of the foot 2,685 in the same space, on the back of the hand 1,490, on the neck and forehead 1,303, on the back of neck and nates 417. The perspiratory glands of the axilla, differing from the others in their considerable size, do not allow of any direct comparison with them, though they far surpass in magnitude those of other portions of the body.

The sweat glands begin to be developed in the fifth month of intra-uterine life, by the formation of a flask-shaped projection of the mucous layer into

the corium, formed of epithelial cells, ending in a dilated extremity. In the seventh month there is an axial canal; in the same month the gland lengthens, its blind extremity dilates and becomes retort-shaped. In the last months of pregnancy this end becomes convoluted into the well-known glandular coil.

MUSCLES OF THE SKIN.— *Voluntary, striped muscular fibres* are found only in the skin of the face, beard and nose; they have their origin deep and are inserted in the corium, sometimes at an acute angle, sometimes at right angles, between the hairs and the sebaceous gland.

Smooth muscular fibres exist in the skin in a twofold distribution. Some run horizontally and form an anastomosing network (Kölliker), as in the scrotum (tunica dartos) and prepuce; some are in crucial bundles, as in the areolæ of the breasts and even in the nipples themselves.

The most common disposition of cutaneous muscular fibres is in isolated bands from 0.045 to 0.22 millim. in diameter, which penetrate the corium in an oblique direction and have special relations with the hair follicles (Haarbalgmuskeln, KÖLLIKER, Erectores pili, EYLANDT). They arise in the outer part of the corium and act obliquely, having their insertion in the inner sheath of the hair follicle. Many hairs have two muscles which cross over the sebaceous gland and surround this in the form of a crescent. The hairs are inserted obliquely in the skin and form a moderately acute angle with the surface, while the muscular fibres occupy the corresponding oblique angle, so that by their contraction the hair assumes a more vertical direction and is somewhat elevated from the level of the skin (goose-skin).

Neumann describes muscular bands, running obliquely in the skin, which have no connection with the hairs.

B. HAIRS—PILI.

The hairs are cylindrical horny structures located in tubular depressions of the skin—the so-called hair follicles—and are developed from a papilla at the fundus of the sac, the hair papilla.

In studying the hairs we must regard: 1, the structure of the hair follicle together with its papilla, and 2, that of the hair itself. In the latter, again, the portion enclosing the papilla, the root of the hair, and the remaining portion, the hair shaft, which projects largely from the skin.

The hair follicle is a depression of the surface of the corium with a blind lower extremity (fig. 223) dilated, and a conical orifice (a). Below the external opening it is narrowed and forms the so-called neck; here it is that the duct of the sebaceous gland discharges its contents.

From the neck to the dilated portion or bulb we distinguish (1) the hair follicle, and (2) the root-sheath.

The follicle proper consists of three layers, an outer, middle and inner. The outer follicular sheath *d* (Kölliker's outer fibrous sheath) consists of compact connective-tissue fibres running parallel to the axis of the hair, which are firmly united above to the fibres, of the corium, and embrace the root below, accompanying, for a distance, the blood-vessels which enter the hair papilla. This sheath gradually merges externally into the connective tissue of the corium without there being any sharp boundary-line, and appears as an independent envelope, 0.02 millim. in thickness, only on that portion of the sac found in the panniculus adiposus. Within this sheath we find two blood-vessels running longitudinally (artery and vein) which encircle

the hair by means of minute inosculations; also here and there nerve fibres dividing dichotomously.

Fig. 223.

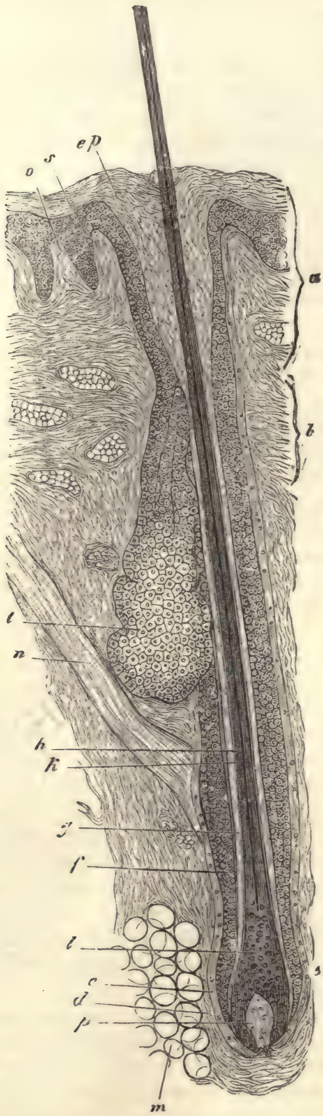

Fig. 223. Hair from the beard. *b*, neck of hair follicle; *a*, orifice; *c*, dilatation of follicle; *d*, outer follicular sheath; *m*, adipose cells; *e*, inner follicular sheath; *p*, papilla; *f*, outer root-sheath; *g*, inner root-sheath; *h*, cortical substance; *k*, medullary substance of hair; *l*, root of hair; *n*, arrector pili; *t*, sebaceous gland; *o*, papilla of skin: *s*, mucous layer; *ep*, horny layer which projects into the cavity of the hair sac.

The middle sheath of the follicle constitutes the inner fibrous membrane of Kölliker (*e*). It consists of scattered transverse connective-tissue fibres, between which there is a homogeneous substance but little granular, with numerous lengthened nuclei placed diagonally. After treating it with nitrate of silver solution several layers of oblong, wavy outlined tessellations appear (Czerny), the nature of which is not yet explained. The fusiform shape and the lengthened nuclei have a resemblance to organic muscular fibres, while for their connective-tissue nature we have the fact that they are isolated with difficulty, and do not swell up nor become opaque on boiling in water (Henle, Kölliker). The contraction of this layer, as after the falling out of the hair, is in favor of its muscular nature (fig. 225). Numerous capillaries enter the inner follicular sheath from the blood-vessels of the outer sheath, and form a dense network. No nerves have yet been found here. This sheath begins at the neck of the hair sac and extends to the fundus, having a thickness even of 0.05 millim. in the coarser hairs of the beard. It is continued below into the hair papilla (*p*), which projects into the cavity of the follicle and generally rests upon a pedicle formed of the inner follicular sheath.

The hair papilla thus presents a constricted neck and expanded body, which terminates in a conical extremity. Its length on the average is twice its breadth. Moreover the length of the papilla is not so proportionate to the length of the hair as is its breadth.

The papilla of the hair consists of connective-tissue fibres coming from the inner sheath of the follicle, between which are numerous round nuclei; round nucleated cells are also clearly discernible. It is quite smooth on its surface, and at its neck is surrounded by the vitreous membrane of the follicle, which cannot, however, be demonstrated on the body and apex. Two small arteries enter the papilla, and, as a rule, unite towards its summit into one stem, subsequently to divide into two efferent vessels (veins). There are abundant anastomoses between these four blood-vessels. I have traced non-medullated nerve fibres as far as the neck of the hair papilla.

The third and innermost sheath of the follicle consists of a transparent layer, the vitreous membrane, from 0.005 to 0.008 millim. in thickness, which is unaltered by acids or alkalies. Although on section it appears perfectly homogeneous, when seen from the surface delicate fibres appear to run diagonally and to decussate; round, faintly outlined nuclei are also seen here and there. A weak solution of nitrate of silver produces a tracing on this vitreous membrane similar to that on the walls of the lymphatics (Czerny*) The outer surface of this membrane next to the inner follicular sheath is smooth, but internally it displays a delicate striation with minute prominences similar to stellate cells (Haight †).

The vitreous membrane is a continuation of the delicate cuticle covering the corium; it invests the whole follicle and is prolonged upon the neck of the papilla, where it becomes thinner and thinner till it is finally lost. It appears, however, that it does cover the body and summit of the papilla, although exceedingly thin in this situation. Neither blood-vessels nor nerves are found in this layer.

The root-sheath (*f*), which we have alluded to as a further constituent of the hair sac, consists of two layers, an outer and an inner. The outer root-sheath (*f*) is formed from the mucous layer which is continued into the follicle; it does not, however, reach its enlarged portion, but ends usually at

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* *Centralblatt für Med. Wissenschaften*, 1869, Nr. 26.

† *Sitzungsbericht der Akademie in Wien*, Jahr 1868, Bd. 57.

the height of the apex of the papilla, or oftener even higher up (Moleschott, Chapuis). It consists of a multiple layer of epithelial cells, of which those nearest the vitreous membrane are for the most part cylindrical, and have round nuclei located nearer to that surface than the other. The cells next to these interiorly are polyhedral, whilst the innermost ones are flattened with oval nuclei.

The outer root-sheath is thinner in the neck of the hair sac, owing to the cells being more compressed there than elsewhere, and it ends, generally, at the expansion of the hair, sometimes being rounded off and consisting of a triple row of cells, and sometimes tapering down so that finally there is but a single row of flattened cells. Between the cells of the outer root-sheath, in chloride of gold preparations, we find here and there dark violet varicose fibres, coming from the vitreous membrane and reaching to the inner root-sheath. The conjecture that these are nerve fibres has not yet been supported by the discovery of any connection between them and the nerves running in the follicular sheaths. Langerhans (l. c.) describes nerve cells, among the cells of the outer root-sheath, similar to those in the rete mucosum.

The inner root-sheath (*g*) consists of two layers, an outer and inner, the outer one being the inner root-sheath of Henle, and the inner the so-called Huxley's membrane. These are quite different structures in reference to their development, texture, and chemical relations; the former is related genetically to the outer root-sheath, while the latter is developed from the root of the hair. The inner root-sheath of Henle appears in a longitudinal section of the hair as a delicate, clear, lustrous layer, resembling the vitreous membrane, and but little colored by the carminate of ammonia. It begins at the neck of the hair follicle and stretches towards the hair expansion only as far as the outer root-sheath extends. Externally, towards the outer root-sheath, the boundary is well defined; internally, it is in contact with Huxley's layer, soon to be described. The former stratum, which Henle was the first to describe and designated the inner root-sheath, consists, however, as both section and direct view show, of oblong lustrous scales without nuclei, lying parallel to the long axis of the follicle, and resembling fusiform cells halved in their long axis. The flat surfaces of these cells touch the outer root-sheath, which they cover continuously; the inner convex surfaces adjoin the cells of Huxley's membrane.

Most anatomists have described small interstices between these scales, which caused Henle to regard this as a cribriform membrane; others have thought that they are only fine splits produced in the preparation of the specimen. There is no doubt but that on flat sections, without any previous isolation of this membrane, there are appearances which seem to bespeak the existence of minute interstices between the scales; but these apparent clefts are caused by the convexity of the cells, which leave larger or smaller intervals in proportion to their shape. By a proper adjustment of the microscope we can readily see that these scales are in immediate contact by the edges of their flat surfaces.

In the deeper portion of the follicle the inner root-sheath consists of a single row of the above-described scales, which are readily distinguishable from the nucleated cells of Huxley's membrane; more externally the former become flatter and the latter lose their nuclei, so that the two layers cannot readily be separated from one another, but it appears that the scales of the inner root-sheath increase in quantity outwards. We may finally mention that those of the inner root-sheath swell up and are finally dissolved in soda and potash.

The *hair* consists of the shaft, its larger part projecting from the surface, and of the hair root, a bulbous expansion of the lower extremity; from the latter are developed a sheath, peculiar to the hair and surrounding the lower portion of its shaft—the so-called Huxley's membrane, and the cuticula of the root-sheath.

Delicate cross-sections of the hair shaft in its natural state show that its edge is finely serrated, and that there are faint lines on the surface corresponding to the apices of the dentations, which enclose oblong quadrilateral spaces. This appearance resembles slightly the surface of the body in the scaly Amphibia, and is produced by small scales dividing up the surface of the hair, representing the so-called cuticula of the hair first described by Herm. Meyer.

The larger part of the hair is made up of the cortical substance (fig. 223, *b*); in gray hairs this is a colorless silvery matter in which numerous dark spindle-shaped granules are found directed longitudinally. In hairs of different hues the cortical portion includes variously colored pigment granules. In the thick hairs of the beard, as also here and there on the head, there is a medullary (fig. 223, *k*) substance within the cortical, which is composed of granular polyhedral cells, and is best studied in gray hairs. The hair shaft ends (on uncut hairs) in a fine point which never has any medulla, and for the most part passes below gradually over into the root of the hair.

The root (fig. 223, *l*) is that portion of the hair which surrounds the papilla and fills the lowest part of the follicle. It is formed of nucleated cells which resemble those of the deepest layers of the rete mucosum, and differ from them perhaps only in a special hardness. Those next to the papilla are cylindrical and are perpendicular to its surface; sometimes they are attached to it by a very slender thread. The outermost cells of the root touch the vitreous membrane and are somewhat flattened; the middle portion is formed of polyhedral cells with quite large nuclei. In the middle of this cell accumulation, at the height of the body of the papilla, we notice a row of cells, running parallel to the vitreous membrane, which are distinguished from other cells by their more compact arrangement, by being somewhat flattened from above downwards, and by being stained more deeply by carmine.

At the height of the summit of the papilla, or sometimes deeper, there appears a line of small scales as a continuation of the cells above alluded to, and this is situated perpendicularly to the axis of the hair, but above the papilla they run more parallel to it, so that the lower ones to a great extent overlap the upper, and only perhaps the sixth part of the outer portion is left free. These scales lying close together and being adherent to each other thus become the cuticle of the hair, as is recognized on the clear border surrounding it and on the finely serrated edge. These cuticular cells, which enter the root of the hair, divide it into a central portion surrounding the papilla, and a peripheral, which lies next the vitreous membrane, and forms at the most the fourth part of the former.

The central portion of the root of the hair, as stated, is composed of cylindrical cells resting upon the papilla, and of polyhedral cells further removed from these. They are marked by their large round nuclei deeply stained by carmine, and by a scanty homogeneous protoplasmic substance. Higher up above the papilla the protoplasma increases in quantity; the cells, as also their nuclei, become at first oval, and those more external become spindle-shaped with lengthened nuclei. In this portion, which generally exceeds the length of the papilla, the hair-root gradually diminishes in size, and is still surrounded by the obliquely disposed cuticular cells. Its component cells are still capable of being colored by carmine.

At a rather sharply defined margin the contour of the individual cells disappears, and fine lines alone are seen, which appear to be the outlines of fibres; the nuclei are also drawn out into threads. The whole mass is no longer stained by carmine, and in gray hairs, from which this description is taken, we have the hard, silvery, horn-like, cortical substance of the hair-shaft. *Thus the central portion of the root, enclosed by the cuticular cells, passes over into the hair substance, the round so-called hair cells becoming more fusiform, and finally being transformed into small horny spindles.*

The peripheral portion, between the cuticular cells and the vitreous membrane of the hair-sac, forms the cuticle of the root and the sheath of Huxley. It consists in the deeper portion of, at least, three rows of cells, the outermost of which correspond to the long axis of the hair, and are drawn out, while those next the cuticle are mostly polygonal, crowd themselves between its scales, and even become metamorphosed into the cuticular scales of the root. These overlap each other in a manner similar to those of the hair cuticle, with the difference that in the latter the upper cover the greater part of those situated below, or in other words, the free uncovered surface of the scales of the hair cuticle is exposed above, that of the root cuticle below. These two cuticular layers are firmly adherent, and when a growing hair is pulled out, both generally follow, together with the inner root-sheath, and only in rare cases does the hair come out alone, with the enveloping cells turned downwards.

The peripheral cells of the hair-root at the height of the body of the papilla are elongated in the direction of the axis of the hair into fusiform cells, and filled below with scattered, above with abundant shiny granules which generally surround the shrunken nucleus. Deep in the follicle these cells are in contact with the vitreous membrane; more externally they touch the inner root-sheath of Henle, before described, and consist of spindle-shaped epidermal cells without nuclei.

The cells in these two localities differ from each other, in that those deeper down always contain a nucleus, are shiny, and filled with granules which are readily colored in carmine, while the others have no nuclei, and are not affected by carmine.

The outermost cells of the hair-root, then, represent a proper sheath of the hair, that first described by Huxley, and called by his name. This membrane consists of nucleated fusiform cells, filled with lustrous granules to the point where the hair still consists of separate nucleated cells which are soft, and imbibe carmine. Higher up the component cells have no nuclei, the granules seem to have united, and it appears homogeneous on longitudinal section, resembling the vitreous membrane, and unites with the inner root-sheath of Henle to form the single inner root-sheath of other authors.

This inner layer, formed by the union of the inner root-sheath of Henle with that of Huxley, extends to the neck of the follicle, where most writers assert that it ends in fibres. But successful longitudinal sections show that the inner sheath is continued into the neck of the sac, it being possible to trace both its internal and external outline into the neck of the hair follicle, although they approach very closely together. Its cells flatten suddenly on entering the neck, and form epidermal cells which overlie the outer root-sheath in several layers, likewise consisting of flattened cells. In some instances, however, it happens that this sheath passes unchanged with the hair through the neck into the orifice, but in most cases the scales composing it mingle with the epidermal scales in the outer opening.

The topographical arrangement of the various sheaths of the hair can only be studied in successful longitudinal sections. Large gray hairs are best

suited for this purpose, as they can be divided lengthwise, and the absence of pigment allows the individual cells of the hair substance to be more easily followed. Preparations made by teasing with needles and cross-sections then complete the study.

Inasmuch as the hair papillæ are located at different depths in the corium, we never obtain similar sections of all the hairs in any cut made exactly parallel to the surface; the appearance will vary according to the height of division of each hair. One section will present a papilla composed of connective-tissue fibres surrounded by a multiple layer of epithelial-like cells, and enclosed by the vitreous membrane; we have here the neck of the papilla enveloped by the cells of the root, neither the cuticle nor Huxley's sheath being distinguishable. The outer root-sheath is also absent.

In another section we have the medullary substance of the hair consisting of oblong quadrangular cells within the cortical substance composed of nucleated polyhedral cells. The peripheral portion is surrounded by many fine lines concentrically arranged, between which delicate oval cells are seen (cuticular cells of hair and root). External to these we have a layer formed of a double row of cells in which there are numerous shiny granules and also marked nuclei (Huxley's sheath), enclosed by a single row of transparent hemispherical cells without nuclei, and not colored by carmine (inner root-sheath of Henle), which is surrounded by the epithelial cells resting upon the vitreous membrane (outer root-sheath). This section passes through the yet soft root over the papilla, at a distance not exceeding its length.

In a third specimen (fig. 224) the hair structure consists of a hard, horny, homogeneous substance in which there appear to be small round nucleoli *e* (divided nuclei of hair cells). The periphery is lighter and displays an indistinct striation, *h* (hair cuticle). This is surrounded by a single row of shiny hard cells enclosing shrunken nuclei, *g* (Huxley's membrane). Next to this lie the cells of the inner root-sheath *f*, without nuclei (Henle's), and the epithelial cells of the outer root-sheath, *e*. The cut is made through about the middle third of the hair sac.

Fig. 224.

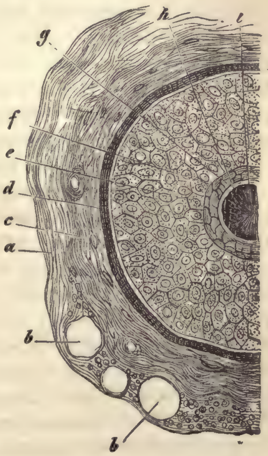

Fig. 224. Section of hair beneath the neck of the follicle. *a*, outer follicular sheath with divided capillaries *b*; *c*, Inner sheath of follicle; *d*, vitreous membrane of the follicle; *e*, outer root-sheath; *f*, scales of inner root-sheath of Henle; *g*, scales of Huxley's membrane; *h*, cuticle of hair; *l*, hair.

In other sections of hair the cells of Huxley's membrane are without nuclei and cannot be distinguished from those of the inner root-sheath; a double or triple row of cells destitute of nuclei surrounding the hair shaft. In this case the hair is divided beneath the neck of the sac.

At the neck of the follicle a quadruple or quintuple row of epidermal cells surrounds the hair shaft. At the orifice of a follicle containing two hairs, each hair is surrounded concentrically by a multiple layer of epidermal cells (altered Huxley's membrane together with the inner root-sheath of Henle), which is again encircled by epidermal strata (horny layers of the follicular opening).

To sum up; longitudinal and transverse sections show: 1, that the horny

substance is developed from the cells of the hair, that is, from the central cells of the root surrounding the papilla; 2, that the cuticle of the hair is likewise formed from the cells of the root; 3, that the cuticle of the root-sheaths and Huxley's membrane are developed from the peripheral cells of the hair-root; and, 4, that the inner root-sheath of Henle corresponds to the horny layers of the outer root-sheath.

The development of the elements of the hair, however, also shows that Huxley's sheath must grow as the hair grows, contrary to Kölliker's assertion; further, that the hair is not pushed forward in the cuticle of the root-sheaths, but between Huxley's membrane and the inner root-sheath of Henle; and that the latter, which corresponds to the newly-formed horny layers of the outer sheath of the root, advances also through the neck of the hair sac.

The agencies producing this are:

1, the new formation of root-cells around the papilla; and 2, the pressure which the hard inner layer of the follicle, contracted about the root-sheaths, exercises upon its contents, crowding them through the orifice.

The cells composing the deeper portions of the root resemble completely those of the rete mucosum in their chemical composition. Acetic acid clears up the protoplasmic substance of the cells, and renders the nuclei more distinct. The cells and their nuclei are dissolved in a short time in weak potash or soda solutions, first swelling up.

In treating hairs with various reagents regard must be had to their strength, temperature, and duration of action (Moleschott, *Untersuchungen zur Naturlehre*, IV. Bd. II. Heft). In concentrated sulphuric acid, after a few minutes the hair cuticle swells to a greater diameter even than that of the hair itself. When warmed to 40° to 50° C. (104° to 122° Fahr.) the cuticle separates into its component cells. This separation takes longer in caustic potash solution of the strength of 4.6 pr. ct. or soda solution of 3 pr. ct. After forty hours the outside layer appears as if surrounded by spines, which are the elevated cuticular cells adhering together at their bases. The cortical portion of the hair, which can be dissected longitudinally by mechanical means, in concentrated sulphuric acid, is separated into its individual scales or lamellæ (fibre cells), from 0.05 to 0.08 millim. in length and 0.01 millim. broad, within which thread-like nuclei, 0.02 to 0.03 millim. long, are seen. The medullary cells are very distinct after several days' treatment with a solution of caustic potash of the strength of two per cent. Stronger solutions of potash dissolve the hair; excess of acetic acid throws down a precipitate of white flocculi which give Millon's and Fourcroy's reaction. Very strong solutions dissolve and decompose the hair; Huxley's membrane, in a caustic potash solution of 4.6 per cent., separates into its component cells without their previously swelling up, in a manner similar to the hair cuticle.

The hair follicles vary in length with the length and thickness of the hairs. Those belonging to the long hairs of the head and the large ones of the beard extend even into the subcutaneous tissue, those of the larger hairs of the rest of the body into the deeper portion of the corium, while the papillæ of the finest downy hairs (lanugo) are located in the more superficial portion. They are never inserted perpendicularly but always form an angle with the surface. However different may be the length and thickness of the hairs, the component parts nevertheless will always be found as above described.

The various hues of the hair depend principally upon the pigmentary contents of the hair cells, which either are filled with a granular pigment or

are uniformly permeated with a coloring substance. But the color of the hair also depends on small air vesicles which exist either between the scales of the hair and the medullary cells, or within them.

Langerhans asserts that the hair papilla is surrounded by a great quantity of double-contoured nerves. In chloride of gold preparations it can be shown that varicose nerve fibrillæ, from the non-medullated fibres which enter the papillæ with the blood-vessels, pass between the cells of the root and here run parallel to the papilla, perhaps as high as its summit.

Development and Interchange of Hair.—The first trace of the hair follicle and outer root-sheath is found in the Human embryo at the end of the third or beginning of the fourth month, in the form of a nodular depression of the surface of the corium into which the cells of the rete mucosum are prolonged, completely filling it. A digital prolongation of the cells of the mucous layer is formed, having no proper sheath, but being enclosed by the fibres of the corium. The next step is the development of a short projection from the fundus of the former, which is about half its size and is likewise formed of cells.

Between these cells, which are distinguished from the former by the nucleus being surrounded by a small amount of protoplasma, we soon find blood-vessels, and recognize this latter formation as the beginning of the hair papilla, which, except in the downy hairs, is marked by its richness in cells.

Around the papilla thus formed spherical cells rapidly accumulate which distend the follicle deep down and cause an excavation in the mucous depression. These cells now, being transformed into long spindles, crowd into the cellular mass formed by the inversion of the mucous layer, and press the component cells sidewards, forming thereby the outer root-sheath. Those around the papilla form the root of the hair, from which the hair itself and Huxley's membrane are developed. Those nearest the papilla become hair cells and remain soft, while those at the apex of the hair, yet being within the outer root-sheath, are horny. This condition of affairs has caused some observers to conclude that the point of the hair was first developed and the root subsequently; others, on the contrary, have thought that the central cells of this inverted portion of the rete mucosum were transformed into hair cells.

The peripheral cells of the hair-root go to form the scales of Huxley's membrane, which also covers the end of the hair. Both are seen for a while surrounded above by the cells of the mucous layer within the outer root-sheath, and gradually this mucous layer, together with the epidermis, is pierced by the growing hair, as is the outer root-sheath, and the point of the hair appears enveloped by Huxley's membrane. Finally the hair seems to grow more rapidly than the latter and ultimately penetrates this also.

The development of the hair follicle has not yet been accurately studied.

The first germ of the hair does not appear on all parts of the skin at the same time, and it seems that a variable length of time is requisite in different places from the development to the eruption of the hairs. Those of the eyebrows and the cilia first are seen, later those on the head, and those of the rest of the body last. Most of the hairs are above the surface by the 24th week. The embryonic hairs here described are always downy, and have, accordingly, short follicles. On many parts this form of hair remains, but on others coarser hairs are subsequently developed, taking the place of these fine lanugo hairs.

When a large permanent hair, whose papilla will reach even into the subcutaneous cellular tissue, is about to take the place of a fine downy hair, whose papilla is located only in the centre of the corium, a lengthening of the follicle of the downy hair must necessarily occur. This happens, as Kölliker first described, by the development of a prolongation of the root-sheath into the deeper layers of the corium. In the same manner as in the first germination of the hair, a hair papilla is formed at the fundus of the epithelial inversion around which the cells of the hair root collect. From them the hair and Huxley's membrane are formed, which penetrate between the cells of the epithelial inversion and occupy the follicle together with the downy hair. The papilla of the latter seems to atrophy and the hair falls out, leaving the large permanent hair in its follicle. This process of interchange of hairs probably takes place not alone during the first year, but repeatedly during childhood, while the skin is increasing in thickness.

The permanent hair grows to a certain length which varies according to the individual and the part of the body. When the hair has reached its proper growth the papilla is no longer capable of sustaining its weight and the hair falls out, to be replaced by a new one. This is the physiological reproduction of hairs, which is typical in Man and occurs periodically in the lower animals.

Fig. 225.

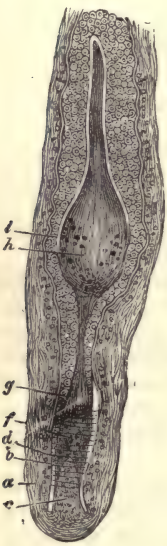

Fig. 225. Falling out of hair after typhus fever. *a*, outer, *b*, inner follicular sheaths; *c*, papilla of hair; *d*, vitreous membrane; *g*, outer root-sheath; *h*, hair bulb connected with the papilla by means of a filamentous band *f*; *l*, outer root-sheath terminating over the hair bulb.

The hair falls from a lack of the production of new cells around the papilla. The root cells last formed, which are not followed by others, are now transformed into hair substance and form either a conical or globular extremity consisting of the fibrillated scales of the hair. Most anatomists, following Henle, have described this rounded end of the falling hair as a particular form of root, Henle's hair bulb, but without reason, for this globular shape is nothing but the end of the hair shaft, which has ceased to grow.

The follicular sheaths, which in consequence of their muscular composition exercise a constant pressure upon the contents of the sac, are continually tending to crowd the hair bulb, together with Huxley's membrane, outward, and contract in such a manner as to press the vitreous membrane directly upon the papilla, and, higher up, to cause the walls of the follicle to touch (fig. 225). The new hair is developed from the old papilla (Langer*).

The hair is lost under morbid conditions, either from the failure of development of new hair, or by the production of downy hair in the place of that which was thicker.

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* *Denkschriften der K. K. Akademie*, 1850. (Fig 191.)

c. Nails—Ungues.

The nails are horny, elastic, translucent, concavo-convex flattened structures, which are embedded in furrows of the skin on the last phalanges, covering a large portion of their surface. In the study of the nails we will consider, (1) the nail itself; (2) the portion of skin covered by it, the nail-bed; and, (3) the cutaneous wall enclosing the nail on three sides—the furrow, *vallecula unguis.*

There are four borders, an anterior or free, a posterior, and two lateral which are inserted beneath the skin; further, a convex external surface, for the most part free, and a concave under surface lying upon the nail-bed. The posterior portion of the nail inserted beneath the skin is its root; the rest is called its body.

The surface of skin covered by the nail, the nail-bed, is divided into a posterior portion covered by the root of the nail, the *matrix unguis*, and an anterior portion, the true nail-bed. The skin bounding the edges projects over the nail, forming the so-called nail wall, and this posteriorly is the broadest, growing narrower anteriorly, and, together with the nail-bed, constitutes what is known as the furrow of the nail. The bed of the nail passes over anteriorly into the skin of the ball of the finger, and at both sides and posteriorly it merges into the under or inverted surface of the wall of the nail. It consists of subcutaneous cellular tissue, corium, and rete Malpighii. The subcutaneous tissue of the nail-bed differs from that of the neighboring parts in its lack of fat, and also in the course of the ascending connective-tissue fibres which are directed backwards towards the root, and which, moreover, proceed from the periosteum of the last phalanges in separate bundles, spreading out in tufts above. Between these bands there are spaces filled with loose tissue, sometimes containing a few fat cells, and including numerous vascular loops.

The corium of the nail-bed, in reference to the direction of its fibres, is similar to that of other parts, only the number of ascending fibres exceeds that in other places, the reverse existing in the corium elsewhere. The most important difference between the corium of the nail-bed and that of the rest of the body lies in the arrangement of its surface, which, however, is differently formed at the posterior part, which we have designated as the matrix unguis, from what it is anteriorly in the true nail-bed. The surface of the matrix, which is situated somewhat deeper than the true nail-bed, is covered with papillæ, 0.1 to 0.2 millim. high and 0.03 to 0.06 millim. broad, placed longitudinally (Henle) upon low ridges of the corium. The surface of the true nail-bed, on the other hand, is covered with from 50 to 90 ridges, 0.1 or 0.2 millimetre in height. These elevations, which are continuations of the wall-like prominences of the matrix of the nail, increase in height towards the free border of the nail, and at its edge pass over into papillæ which are even 0.5 millim. in length. The projections consist for the most part of perpendicular connective-tissue fibres ascending parallel, between which are embedded numerous fusiform cells.

The blood-vessels form a coarse plexus in the corium of the matrix, from which loops enter the papillæ; in the nail-bed proper, on the contrary, the network is finely reticulated and numerous large vessels ascend to the ridges.

In the subcutaneous tissue of the nail-bed there are abundant medullated nerve fibres which lose their medulla at about the line of the corium and then ascend perpendicularly to the surface. I once followed a fibre of this

kind, in a chloride of gold preparation, as far as the surface of the corium, from which, however, the mucous layer had become separated in its preparation; I could find no nerve fibres in the latter. The corium of the nail wall on its upper surface is like the skin of the back of the finger, and that beneath (turned towards the nail) is smooth and has no papillæ nor glands.

The mucous layer of the nail-bed is in no way different from that of the rest of the skin. It fills all the depressions of the nail-bed, therefore occupies the spaces between the papillæ of the matrix and the furrows betwixt its ridges, merging directly into the rete mucosum of the adjacent parts, that is, into that of the nail wall. At the posterior angle of the nail furrow the mucous layer of the matrix joins with that of the wall in such a manner that a cuneiform portion projects into the corium, which rests on the periosteum and is firmly adherent to it by means of short, firm connective-tissue bands.

The deepest cells of the rete mucosum of the nail-bed are cylindrical, the middle polygonal, the outermost flattened. All of them enclose large, clearly defined nuclei. The further destiny of the cells of the mucous layer of the nail-bed varies. In the true nail-bed they pass suddenly, as in other locations on the skin, into flat epidermal scales; over the matrix they are gradually changed into the nail substance.

A vertical section dividing the nail into two lateral halves shows that the layers of nucleated flattened cells over the matrix are much thicker than over the nail-bed proper, and that over the matrix they pass into the horny substance of the nail in an oblique furrowed surface. The thickness of this layer gradually decreases toward the extremity of the joint as the thickness of the nail substance increases. The boundary between the mucous layer of the true naii-bed and the substance of the nail is sharp and even, and in most cases there is between them a thin stratum of loose epidermal cells (visible in chromic acid) which also increases in thickness towards the free border of the nail (Reichert).

Fig. 226.

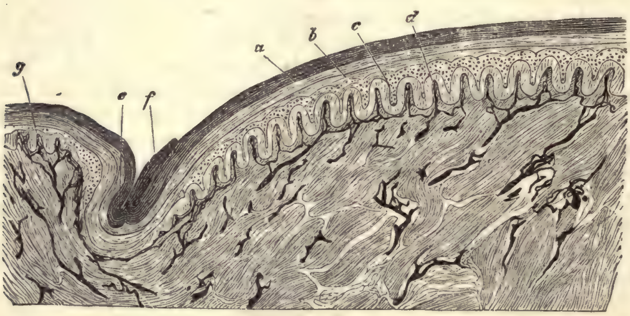

Fig. 226. Section of a nail through the true nail-bed. *a*, nail substance; *b*, loose horny matter beneath the same; *c*, mucous layer; *d*, divided ridges of the nail-bed, with injected blood-vessels; *e*, nail furrow, without papillæ; *f*, horny layer of the nail furrow, extending over the nail; *g*, cutaneous papillæ of the back of finger.

There is no well-defined boundary between the mucous layer of the matrix and the root of the nail, the outermost flattened cells of the rete

mucosum of the matrix passing gradually into the more and more flattened, nucleated, sharply contoured nail cells, which are colored by carmine, these again changing into very flat scales in which the nuclei are no longer visible. These are further transformed into a homogeneous, shiny, horn-like nail substance, not stained by carmine but rendered greenish in chromic acid. The mucous layer of the under surface of the nail furrow turned towards the nail is covered by a layer of epidermis increasing in thickness towards its extremity, which lies upon the upper surface of the nail but is readily removed from it, and which therefore does not participate in the formation of the nail.

The rear portion of the nail-bed, which lies in the nail furrow and is provided with papillæ, must therefore be considered as the only place of formation of the nail, and is consequently rightly called the nail matrix. It corresponds to the hair papilla, while the nail furrow answers to the hair follicle and directs the growth of the nail anteriorly. The nail cells increase in breadth from below, but since they cannot extend symmetrically on account of the enclosing walls, they must advance, pushed forward by the new cell-production. For this reason the nail cells have a tile-like arrangement, the upper covering the greater part of the under, leaving only the posterior border free (Virchow).* When the nail furrow is absent, as often occurs on the little toes, the nail increases only in thickness in the form of a horny lump, which reaches a certain height and then breaks off.

A suppurative inflammation of the matrix of the nail leads to a temporary or permanent loss of the latter, according as it is replaced or destroyed entirely. The nail is formed from the matrix and is pressed forward from behind over the nail-bed. Suppurative inflammation of the true bed of the nail does not interrupt its growth; often the nail will not touch its bed at all and yet preserve its normal thickness.

The nail substance, which appears homogeneous on section, with at most a fine striation, and which refracts light, consists of epidermal scales very closely united, which may be separated into its elements by various chemical agencies. According to Moleschott, ammonia dissolves the uniting substance in twenty-four hours. The cells are irregularly polyhedral and enclose a round nucleus. Ammoniated copper in strong solution makes the scales of the nail polyhedral in an hour and a half, and in two or three hours causes them to swell up into an elliptical form. The nucleus takes up this solution quickly.

The best way to procure isolated nail cells with distinct nuclei is to soak them in a lye of potash 27 per cent. The nail in this becomes quite soft and a thin section gives a satisfactory view. The body of the nail is streaked longitudinally and has ridges on its surface which, however, must not be understood as impressions of the lines of the nail-bed (Kölliker), but as a consequence of the papillary structure of the matrix; for the root of the nail also is ribbed.

Development of the Nail.—In the third month of fœtal life an elevation of the skin of the last phalanx is noticed, concave in front, which corresponds to the furrow of the nail, and is produced by the mucous layer sending out into the corium a ridged projection on a line parallel to this wall This prominence consists of a double or triple row of epithelial cells like those of the mucous layer.

In the fourth month there is a double or quadruple row of flat, very

* *Zur normal. und path. Anat. der Nägel.* Würzb. Verhandl. B. V.

sharply defined, nucleated cells between those above described, which correspond to the nail cells. At this time the skin enclosed by this wall, and which is to become the bed of the nail, resembles completely that of other parts. In the fifth month these nail cells crowd forward between the mucous and horny layer of the nail-bed, so that the newly formed nail is still covered with the horny layer and has no free border.

When the nail reaches the end of the finger, in the sixth month, beneath the horny layer, it lifts this off in the form of a pouch, open posteriorly.

CHAPTER XXVII.

THE SEROUS MEMBRANES.

By E. KLEIN.

Serous membranes in general are composed of an endothelium, a basis substance, lymph-vessels, blood-vessels, and nerves.

a. Endothelium.

All serous membranes carry on their free surfaces a single layer of cells; the Mesentery, the serous portion of the Diaphragm, and to a certain extent the external layer of the Pericardium possess accordingly an endothelium on both surfaces, while the Peritoneum parietale, the Pleura, the visceral layer of the Pericardium, and the Dura Mater possess it only on the surface which is turned towards the serous cavity. As regards the Pericardium, I would state that the cellular covering of its outer surface is an imperfect one; in the Rabbit, the Cat, and the new-born Infant it extends over a large part, in the Guinea-pig over the largest part of the outer surface.

According to Böhm (1) the Dura Mater possesses an outer cellular covering only in the Rabbit.

In the Triton and Frog small ciliated pavement cells are found scattered either singly or in groups among the non-ciliated cells on the Peritoneum parietale, the Mesentery, and also, in the latter animal, on the peritoneal surface of the septum (2) of the Cysterna magna.

The individual cells are somewhat flattened in shape, and possess a round or oblong nucleus, situated often eccentrically: the transverse diameter of the nucleus is usually greater than that of the cell itself, so that at the point where it lies it causes the superposed layer of cell-substance to bulge outwards. As a rule, the more regular the shape of the cell, the more perfectly round will be the form of the nucleus. The endothelial cells are quite uniformly polyhedral in the Mesentery of the Rabbit and new-born Infant, in that portion of the Peritoneum of the Frog and Cat which covers the stomach and the intestine, and on the thoracic side of the Centrum tendineum of the Guinea-pig.

The cells are most irregular in shape in the Mesentery of the Frog, and also to a certain extent in that of the Cat; they here almost always possess an irregular form, and consist of more or less elongated plates, which are always provided with sinuated borders; hence the boundary-line between any two adjacent cells is characterized by several larger and smaller curves. The long diameters of the elongated cells of both surfaces cross each other in the same manner as do the cells of the opposite walls of a larger lymph-vessel.

The nucleus of these endothelial cells very rarely occupies a central position; it is usually oblong in shape, and at the same time shows depressions either throughout its whole surface or only over one-half of it. It is not a rare circumstance to find elongated cells with several projections at both poles, and containing two nuclei.

In the Pleura, the Pericardium, and the Centrum tendineum of the Diaphragm there are found, in addition to the cells of irregular polyhedral shape, others which possess a more or less irregular form—triangular, oblong quadrangular, and elongated cells of irregular shape. As to the size of the individual cells and the character of their outlines there also exists the greatest variety. At one time they will be found of equal size over quite a large extent; at another, groups of absolutely small cells will be found among a few large ones; in these places transitional forms between the two may or may not exist. These last-mentioned relations may be seen beautifully exhibited in the Pericardium of the Cat, also in the Pleura intercostalis (3), and over the lymph-vessels on the abdominal side of the Peritoneum (4). As regards the boundary outlines of the endothelial cells, their form in silvered preparations differs in different places: in the Mesentery of the Frog and Cat, on the abdominal side of the Centrum tendineum, above the fissures of which we shall speak hereafter, and also in certain spots on the inner surface of the external pericardial layer of the Rabbit, the contours of the endothelial cells follow a very marked serpentine course; the same outlines, though not so decided in character, may also be seen in certain spots of the Pleura and on the thoracic side of the Diaphragm. It is worthy of mention that in silvered preparations the cell-contours are much more delicate over the (hereafter-to-be-mentioned) broad fissures on the abdominal side of the Centrum tendineum and over the lymph-vessels of the Pleura (5) than in the intermediate places.

The arrangement of the endothelial cells is either a simple juxtaposition of polyhedral cells, or, where they are elongated in shape, they fit into each other with their drawn-out ends; or they may be arranged in groups of from four to ten, like radii around a common centre. This last arrangement may be observed on the abdominal (6) as well as the thoracic side of the Centrum tendineum of the Diaphragm, on the Mesentery, on the abdominal surface (7) of the septum of the Cysterna lymphatica magna of the Frog, on the Pleura (8), and on the inner and outer surfaces of the Pericardium of the Rabbit, Cat, and Man, and also on the Dura Mater of the Rabbit (9).

In the centre of these groups of endothelial cells there are found one or even several (2 and 3) sharply outlined, round, or triangular spots of varying size, which, since the time of Recklinghausen's and Oedmanson's discoveries, have been looked upon as openings between the endothelial cells —the so-called *stomata*. Then again in these same localities we find groups of endothelial cells arranged in a radiating manner, in whose centre the stomata referred to above are wanting.

In silvered preparations we find between two or more endothelial cells smaller spots of variable size, which occur either singly or in groups, and whose outlines are always sharply drawn. In some places, moreover, it is almost impossible to decide, owing to the absence of nuclei and the presence side by side of figures of such various sizes, what should be considered as a stoma and what as a smaller endothelial cell. In view of these facts, investigators have all maintained that silvered preparations did not afford an actual proof of the existence of openings between the endothelial cells. The places referred to, however, are assumed to be stomata, on the ground of Recklinghausen's experiments (10), which were also repeated by Ludwig and Schweigger-Seidel, by Dybkowsky, by Schweigger-Seidel and Dogiel, and by Böhm. Moreover, the presence of stomata is clearly indicated by the successful injections of Dybkowsky (see fig. 8. of his treatise).

From an histological stand-point we can, strictly speaking, consider as stomata only those small figures which are found in the centre of a radiat-

ing group of relatively large endothelial cells; in such places we can with a little care usually find—as did Schweigger-Seidel and Dogiel (10) on the abdominal surface of the septum of the Cysterna lymphatica magna—the nuclei of the cells that bound the stoma in question lying at the periphery, close to the stoma. All the other small figures, whether they appear in groups or singly, very probably represent young cells, which, by the process of subdivision, have come from larger endothelial cells. The following circumstances favor this view: the appearance in the Mesentery of the Frog of endothelial cells with two nuclei, and the discovery of nuclei which are on the eve of subdivision by constriction; the peculiar irregular shape of these endothelial cells, which look very much as if during life they had undergone changes in form; the fact, as stated above, that in some places several small cells are found inserted between some of the larger ones; and, finally, the discovery of Ludwig and Schweigger-Seidel, that on the abdominal side of the Centrum tendineum of the Rabbit all stages of nucleus-subdivision may be observed in the endothelial cells. Ludwig and Schweigger-Seidel consider these groups of cells, which have emanated from the endothelial cells by the process of subdivision, as lymph corpuscles.

The Omentum majus of the Cat consists of a very ornamental connective-tissue framework containing openings, which are found to diminish in size as we approach the principal trabeculæ, those namely that carry the vessels. The endothelium adapts itself perfectly to every part of this framework.

The best methods to employ in the investigation of the cellular coverings are the well-known silver method and maceration in iodized serum.

b. Basis Tissue.

The stroma of serous membranes consists of connective-tissue and elastic tissue. The former is composed of wavy fibres collected together into bundles, which generally form a beautiful meshwork; these interweaving bundles pursue a varying course, and in some places form more solid trabeculæ, in which larger blood and lymph vessels and nerve trunks lie embedded. The same disposition of the connective tissue may be seen in the Mesentery, in the delicate basis membrane which in the Pleura lies beneath the epithelium (12), and in that of the abdominal and thoracic sides of the Centrum tendineum.

In other places the connective-tissue stroma manifests a more tendinous character—as, for example, in the Centrum tendineum, which in the Rabbit consists of two layers, a circular on the thoracic, and a radiating (13) on the abdominal side; in the Pericardium, to a certain extent; in the deeper layers of the Pleura intercostalis, and in the Dura Mater.

With this connective-tissue meshwork is interwoven a close network of delicate elastic fibres, which run mostly in a straight or slightly curved line, more rarely in a strongly curved or serpentine course. The bulk of these plexuses of elastic fibres—which, it should be mentioned, may lie in more than one plane—is very variable: it is greatest in the Mesocolon of Mammals and Man, and in the Mesentery of the Guinea-pig; it is always abundant in the Mesentery of the Frog and Mammals, in the Pleura, in the Pericardium, in the basis membrane which covers the circular layer, and also in that covering the radiating layer of the Centrum tendineum of the Diaphragm.

Adipose tissue occurs in larger or smaller masses in the Mesentery and Pericardium; in the former locality it is generally found only in the larger trabeculæ (and their branches), which run in a radiating direction from the

root of the Mesentery to the intestine, and correspond to the ramifications of the larger blood-vessels. As in all connective-tissue organs, so here too, numerous cellular elements are found scattered among the fibres. These are of different kinds: in the first place there are branching cells with rounded nuclei, which by means of numerous simple or branching protoplasma-processes constitute a close network; there are also larger and smaller rounded or irregularly shaped granular masses of protoplasm, each of which possesses one or more nuclei; then there are spindle-shaped granular cells, with round or oblong nuclei (these are frequently seen between the straighter connective-tissue bundles of the middle layer—radiating and concentric layer—of the Centrum tendineum, in the deeper layers of the intercostal Pleura, in the outer layer of the Pericardium, and in the Dura Mater); finally, wandering cells are also found here. The substance of the Peritoneum, in many Vertebrates, contains bundles of smooth muscular fibres, which either occur separately or are united in the form of a network; these are especially abundant in the Mesentery of the Triton and Frog; they are also present, though in smaller numbers, in Mammals; at the same time even here spots may be found where the muscular fibres occur in large numbers, as for instance in the peritoneal covering of the Rabbit's stomach.

For the study of the fibrous elements of serous membranes, sections of objects hardened in chromic acid will be found to answer the purpose best (Pleura, (14) Diaphragm(15)), or surface views of portions either of fresh objects or of such as have been previously placed in the Bichromate of Potassa (Mesentery, Pericardium). For the study of the cellular elements we possess in the chloride of gold a most excellent reagent; at the same time fresh specimens may also be studied to advantage.

c. Lymph-vessels.

The existence of serous canaliculi in the connective tissue of serous membranes has been denied by Dybkowsky, Schweigger-Seidel, Ludwig and Schweigger-Seidel; Böhm alone has found them on the internal surface of the Dura Mater. In opposition to Schweigger-Seidel's (13) statement, that the appearances which we recognize as serous canaliculi are an artificial production in the layer of albuminoid glue-substance which separates the endothelium from the basis tissue, Böhm maintains—what is now a well-established fact—that in some cases the endothelium may still be seen in a state of perfect preservation above the outlines, in the basis tissue, of the serous canaliculi. In all the serous membranes that I have examined (the Mesentery of the Triton, Frog, Rabbit, Guinea-pig, Cat, and Man: the Peritoneum parietale of the Frog, Rabbit and Man; the Pericardium, Pleura and Centrum tendineum—on the thoracic as well as on the abdominal side—of the Rabbit, Guinea-pig, Cat, and Man) I have been able to verify in every respect the statements made by Von Recklinghausen concerning serous canaliculi (see figs. 77 and 78 of Chap. VIII.).

According to Dybkowsky the Pleura costalis possesses lymph-vessels only in those portions which lie next to the musculus sternocostalis in an intercostal space; here the lymph capillaries form close networks, which empty their contents into the small valved trunks that run along the border of the intercostal space. The capillary plexuses are arranged chiefly in two layers: the one, which is situated superficially, fills up the interstices in the basis membrane, and the calibre of its vessels is separated from the cavity of the Pleura by only the endothelium; the stomata, moreover, which are found between the endothelial cells, lead directly into lymph-vessels of this layer

(19); the other layer is situated deeper down, being separated from the first by a mass of connective tissue whose bundles run parallel with the plane of the Pleura; both layers anastomose frequently one with the other. That portion of the Pleura which covers the ribs possesses no lymph-vessels whatever. The mediastinum possesses lymph-vessels only in those spots where adipose tissue is deposited between its layers.

In the outer layer of the Pericardium the lymph capillaries form a close network which lies near to the inner surface and receives serous canaliculi from all parts of the basis substance. In the Centrum tendineum of the Rabbit there exists, according to Ludwig and Schweigger-Seidel, a system of broad lymph paths, which are embedded in the radiating layer of fibres and run parallel, side by side; they are lined, moreover, with an endothelium, and are covered by the basis membrane of the abdominal side. This membrane consists of broader bands, that correspond to the spaces intervening between the fissures, and of more delicate cords which start from the bands and form a beautiful meshwork even over the fissures (20).

From these fissures, which belong to the lymphatic system, canals lead to the thoracic side of the tendon, where, between the Pleura and the circular layer, there exists a beautiful close network of lymph capillaries; this network pours its contents into broad, valved lymph-vessels, which also are located on the thoracic side.

In the Centrum tendineum the plexuses of lymph capillaries are most richly developed posteriorly. In addition to these statements of Ludwig and Schweigger-Seidel it should be mentioned that in the Rabbit, Man, and Cat, but especially in the Guinea-pig, it appears that, by the aid of the silver method, a richly developed system of serous canaliculi and lymph spaces, lined with endothelium, may be proved to exist in the delicate basis membrane both of the abdominal and of the thoracic side of the tendon. On the abdominal side of the Centrum tendineum of the Guinea-pig we find that from the trabeculæ of the basis membrane, in which blood-vessels and nerve-trunks may be recognized, smaller cords, corresponding to the ramifications of the blood-vessels, are given off in a pretty straight line, and enclose large broad spaces, which are lined with endothelium. (See fig. 78 of this book.)

These lymph spaces receive from all sides the short, fissure-like serous canaliculi, and also longer narrow canals, which follow the course of the blood-vessels and nerve-trunks, and may even become developed in the adventitia of the former, and broad connective-tissue sheath of the latter.

These very broad lymph spaces communicate with the epithelium-lined fissures which lie between the fibres of the tendinous tissue.

In the Mesentery the larger, valved lymph-vessels are situated in the principal trabeculæ, which run in a radiating direction from the root to the intestinal margin of the Mesentery: these larger vessels receive from all sides lymph capillaries of varying breadth, which (in the Mesentery of the Frog) originate partly from rounded or oblong, broad, epithelium-lined lymph seas, and partly from the serous canaliculi direct. The lymph seas have their roots in the rhombic, stellate, or fissure-like serous canaliculi, and are situated in the midst of smaller connective-tissue cords, which are stretched across between the principal radiating trabeculæ and anastomose with each other by means of numerous smaller bundles of arching fibrils.

In the Mesentery of the Frog, and also on the abdominal side of the Centrum tendineum of the Guinea-pig, blood-vessels and nerve-trunks may be distinctly seen, in some places, lying embedded in lymph spaces; while in others they are simply accompanied on both sides by lymph capillaries.

We should also mention the fact that in the Adventitia both of the blood- and larger valved lymph-vessels of the Frog's Mesentery, very beautiful markings are met with (in silvered preparations), which present the strongest resemblance to the markings of serous canaliculi.

For the study of the lymph-vessels in serous membranes the silver-impregnation method answers well, either in unpencilled, or, better still, in pencilled objects; the vessels may also be injected from the serous cavity.

Further details on this subject may be obtained in the works of Recklinghausen, Dybkowsky, Ludwig, and Schweigger-Seidel.

d. Blood-vessels.

In the Pleura intercostalis and sternocostalis the blood capillaries form, as Dybkowsky has shown, broad meshes, their larger stems following the same course as the lymph-vessels. The capillaries of the Pleura anastomose freely with those of the fascia, down even to the muscles. That portion of the Pleura which covers the ribs appears often to be more richly provided with blood capillaries. In the parietal layer of the Pericardium the larger blood-vessels enter from without and break up near the inner surface into a pretty close network of capillaries.

In the Mesentery the smaller and smallest vessels are given off like the branches of a tree from the larger radiating trunks, and finally break up into a broad-meshed capillary network beneath both surfaces.

In the Centrum tendineum of the Rabbit the large vessels, according to Ludwig and Schweigger-Seidel, usually penetrate beneath the serosa from the thoracic side—more rarely from the abdominal side; the finer twigs pierce the tendinous basis tissue and penetrate as far as to the fissures which lie between the fibres of the radiating fibrous layer; here these vessels seem to be attached to the margins of the fissures, not by their Adventitia, but by a delicate membrane which covers them. In the delicate basis membrane both of the thoracic and of the abdominal side the capillaries form broad-meshed networks.

According to Recklinghausen (21) and Böhm (22) the blood-vessels of the Dura Mater are peculiar in this respect: they form on the outer surface of the membrane a venous network whose branches are disproportionately broad. In the Dog, in particular, the venous branches unite between the arteries to form large sinuated spaces. Böhm has seen these venous networks successfully injected from the inner surface of the Dura Mater, and concludes from this circumstance that an open communication exists between the veins of the external surface of the Dura Mater and the cavitas serosa cranii.

The blood-vessels may be studied even in their finest ramifications, either from injected preparations or from those which have been treated with silver or the chloride of gold; the latter method of preparation is sometimes so satisfactory that we can dispense with the injection altogether.

e. Nerves.

The nerves of serous membranes have been investigated but little. According to Cyon (23) the nerve fibres, which are distributed over the septum separating the abdominal cavity from the Cysterna lymphatica of the Frog, are doubly contoured and surrounded—either singly or two or three together—by a separate sheath. After frequent subdivision they become non-medullated in character and exhibit in their course nucleated swellings.

Broad nucleated fibres possessing a distinctly fibrillated structure may also be seen in those places where the bundle of nerve fibres appears to be spread apart.

The individual fibres frequently intercross and, in some places, are even wound around each other; they finally form a network with broader and narrower meshes, which are mostly rhombic in shape. According to Cyon this network does not represent the termination of the nerve fibres: on the contrary, they extend free, he says, into the substance of the membrane.

In the Mesentery the entering trunks are composed of medullated fibres; they accompany singly or in pairs the larger blood-vessels. Both the trunks and the individual fibres pursue a markedly tortuous course.

The few branches that are given off laterally consist, a certain distance from the main trunk, of one or two non-medullated fibres, which also possess the characteristic protuberant, oblong nuclei. The individual non-medullated fibres finally form a network with rhombic meshes; this network, especially in and near the Adventitia of the larger blood-vessels, is quite close, displaying at its nodal points oblong nuclei.

In the Serosa of the abdominal side of the Centrum tendineum, I have gone no farther than to demonstrate the existence of some larger trunks consisting of non-medullated fibres. These trunks possess nodular swellings and offer the same peculiarity that is exhibited in a beautiful manner in some parts of the Mesentery, *i. e.* they appear to be separated from the adjacent tissues on both sides by a pretty broad lymph space.

In the study of the nerves the silver-impregnation process may be used, or, still better, the well-known method of staining with gold.

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8. Dybkowsky, l. c.
9. Böhm, l. c.
10. See Chap. VIII. of this book.
11. l. c.
12. Dybkowsky, l. c. Fig. 8. 20.
13. Ludwig und Schweigger-Seidel, l. c.
14. Dybkowsky, l. c.
15. Ludwig und Schweigger-Seidel, l. c.
16. Recklinghausen. Die Lymphgefässe und ihre Beziehung zum Bindegewebe. Berlin 1862.
17. See Chap. VIII. of this book.
18. l. c.
19. Dybkowsky, l. c. Fig. 8.
20. Ludwig und Schweigger-Seidel, l. c. Fig. 3.
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CHAPTER XXVIII.

THE MAMMARY GLAND.

BY C. LANGER.

We rarely meet with a mammary gland that is completely matured, and capable of performing its functions, until the Female has arrived at the end of gestation; at this period it consists of a system of arborescent ducts bearing upon their extremities club-shaped glandular vesicles. The main excretory ducts, numbering from fifteen to twenty, are minute little tubes opening singly into the nipple. Before reaching this outlet and while still within the limits of the areola they establish broad and variously sacculated receptacles corresponding with the diverticula given off. These ducts also send occasional recurrent branches under the areola to collect the secretion of the little glandular bodies stored there. Still it occasionally happens that the glandular bodies send their own little excretory ducts to the surface, where they also discharge within the limits of the areola through small prominences patterned after the nipple (glandulæ aberrantes of Montgomery). If it be really true that the branches of one duct form anastomoses with the corresponding branches of another duct, this is not to be regarded as a constant phenomenon, but merely one that occurs in the vicinity of the receptacles.

The terminal vesicles are very closely crowded together and constitute little lobules; on the under surface and at the circumference of the gland they are given off in pairs from the forked branches of a duct; in the centre of the gland, however, and under the areola they represent separate little masses, which often enough are lodged immediately on the wall of a large duct. These little lobules never unite in forming larger lobes, nor is the entire gland subdivided into large lobes corresponding to each separate excretory duct. The reason of this is that the glandular stroma is essentially a connective-tissue body, whose texture is firm and inseparable throughout, excepting only at the periphery; at this point the web is looser, for the purpose of enveloping the glandular lobules and separating them from one another. Thin prolongations of the stroma are given off from the circumference and upper surface of the organ and are continuous with the subcutaneous connective tissue, forming with it niches and meshes which receive the fat surrounding the gland. Accordingly, the nipple is the only point where firm gland-substance is in immediate connection with the skin; here and under the areola there is absence of fatty tissue; in place of it we find a stout layer of smooth muscular fibres.

The structure of the excretory ducts is very simple: first of all, the walls consist of a finely-fibrillated connective tissue; on the outer side this is denser than within, and the arrangement of the fibrillæ is circular; on the extreme outer border elastic fibres are frequently interwoven: in the second place, they have no proper muscular system: finally, the epithelium consists of small cylindrical cells. The larger ducts, when they are no longer furnished with cells, collapse and the walls are necessarily thrown

into folds, so that when seen in transverse section they have stellate or indented outlines.

Glandular vesicles, like glandular ducts, have but one layer of epithelial cells; these at the fundus are short and polyhedral; at the outlet they are somewhat taller and sometimes encroach upon the calibre. The entire cavity of the vesicles is filled with fat globules—anatomical elements of the milk—and though these receptacles may easily be emptied of their contents, yet a number of the little drops always remain adherent to the epithelium and some are even found arranged in rows between the nuclei. In Women that have died shortly after childbirth, the glandular vesicles have occasional milk corpuscles only and these are deposited between the tightly packed epithelial cells. If the fatty matter be removed from the contents of the vesicle by means of ethereal oil, we observe a curdled caseous substance remaining which is spread out in the form of a network, traversing the acinus in all directions. The meshes correspond to the destroyed fat-globules.

Fig. 227.

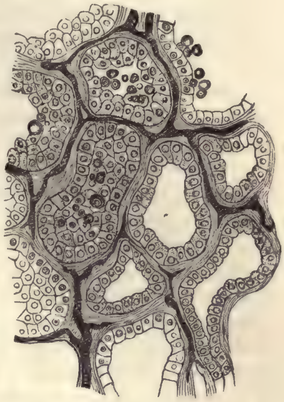

Fig. 227. Transverse section through the terminal vesicles of the gland in a nurse, showing the blood-vessels. System No. 8. Hartnack.

Another element in the parietes of the glandular vesicles is a reticulated connective tissue. The cellular components of this tissue, provided with nuclei and processes, form a little basket which confines the acinus, and is seen when the epithelium is removed: such structural elements have already been demonstrated in the lachrymal and parotid glands (Boll*). The connection of this network with the interalveolar cords can be readily shown; notwithstanding, I was unable to establish positively whether outrunners were given off to the epithelial cells or between them. There is still another question as to the relations of this network to the apparently structureless membrane which is exposed after macerating the lobules. This question I shall be obliged to leave unanswered.

Fig. 228.

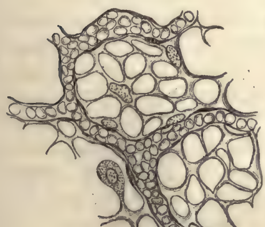

Fig. 228. Reticulated connective tissue apparently connected with an epithelial cell. From the walls of two glandular vesicles. Immersion System No. 9. Hartnack.

The large vascular trunks are all distributed in the subcutaneous connective tissue; it is only the smaller vessels that penetrate the organ, which they do at the under surface: the largest of these latter vessels pierce toward the nipple, furnishing branches at intervals to the gland-substance and small twigs that are destined for the skin: finally the last branches of the smaller vessels, which have pressed forward quite to the base of the nipple, furnish ascending and descending branchlets. The vessels supplied to the parenchyma are not invariably destined for the corresponding ducts; on the contrary, the vascular supply of the two is usually independent, and accordingly each separate gland-lobule takes up and gives off its vessels at its own periphery.

* M. Schultze's Archiv. V. p. 334.

The capillaries of the small lobules constitute a three-sided network. In the meshes, which are rounded or angular, the glandular vesicles are inserted, and hence upon transverse section they are found between the narrow interalveolar cords. It is easy to demonstrate that this capillary network represents an entire system in itself, and that small arteries and veins furnish the sole means of communication between neighboring lobules.

The ducts, also, have a capillary system of their own, distinct from that supplying the stroma; these are minute little vessels which meet in long meshes, as a pretty close though still delicate network. Accordingly, erectile-tissue formations do not occur in the nipple, nor, too, are either the vessels of the stroma or the muscular bands of extraordinary size. Lastly, the capillary loops of the papillæ are also given off from especial stems which lie close under the papillæ, and here at intervals pursue an arching course. Under the areola the veins of the nipple form a circular anastomosing chain, known as the Circulus Halleri.

As to the Lymphatics and terminal Nerve-apparatus of the mammary gland, nothing as yet has been determined.

The first indications of a rudimentary lacteal gland appear perhaps as early as within the third month of intra-uterine life; and yet, in new-born Children we usually find the principal ducts only, though we then observe upon each duct two or more club-shaped appendages, indications of subsequent branches. Now, should there be a still further advance in the growth of these branches, even then the terminal vesicles will always be absent, and the same is true even where a secretion takes place; in this latter case, however, we find numerous dilated sinuses closely crowded together, giving to the gland the appearance of a group of sebaceous follicles.

Until puberty there is but a slow increase in the number of ducts, even in the Female; it is only during puberty that a more rapid growth takes place, the results of which become permanent in Women; in Men, on the other hand, it is possible that a retrogressive metamorphosis may take place. Accordingly, in Men we generally find only the principal ducts with some knobbed and slightly-branched diverticula; still cases have occurred where the glands have developed to the size of a walnut, containing a variously ramified system of ducts formed as in the Female before she has arrived at sexual maturity.

Fig. 229.

Fig. 229. Transverse section of glandular vesicles in a Virgin. The luminous circles have a swollen appearance. System No. 8. Hartnack.

The true glandular vesicles that serve as the termini for a system of ducts already variously ramified can only be found in Women who have reached maturity. At this period of life the gland has begun to show an acinose or clustered form, still the lobules are not very voluminous; they are also widely separated from one another; all the ducts, too, are narrow, and the vesicles are small and cylindrical, rather than club-shaped. In the Virgin the contents of the entire system of ducts consist of cell-masses; these are packed tightly together at the termini and represent a solid mass, but in such passages as are permeable they constitute the single investing coat. A finely-fibrillated connective tissue also enters into the composition

of the walls in the larger ducts, but the limiting membrane in smaller ducts is a layer of hyaline connective tissue capable of swelling to a great extent. The membrane is separated from the stroma by a row of slender spindle-shaped little bodies. At the extreme ends this layer appears thicker, and exhibits on transverse section broad luminous circles, swollen in appearance. The outer and sharply defined borders are crowded against one another, while the inner show slight depressions, evidently to be regarded as an appearance solely due to the swelling.

The stroma of the gland during its development consists of tendinous bundles of connective tissue containing single spindle-shaped little bodies; these bundles are so intimately interwoven with one another that they constitute an indivisible mass, tough as india-rubber. It possesses numerous little canals for the passage of ducts and larger vessels. The compact tissue is everywhere traversed by a mesh of capillaries, chiefly, however, destined for the ducts. The rounded extremities of the still growing canals are grasped by a whole bundle of vessels, for these vessels, on arriving at the duct, diverge so as to embrace it; they then accompany it a short distance. In such cases, therefore, the vessels constitute fibrous appendages, which also obviously indicate what direction the ducts will assume in growing. It is not so with the matured lobules, for they are surrounded and traversed by a network of capillaries.

Fig. 230.

Fig. 230. Terminal buds of the ducts, showing the vessels. From a Girl 14 years old. System No. 4. Hartnack.

Among the capillaries of the stroma there are not a few which are richly provided with nuclei; from some, too, we see very delicate threads given off, which are scarcely yet pervious, and obviously represent capillaries in the stage of development. I could distinguish nerves, too, small in size, and consisting of from two to three medullated fibres; I also saw fibrils which, after separating from their fellows, divided in a forked manner. In the interior of the vascular bundle which was given off from the blunt-end of the duct-branch I saw one of these fibrils, which could not be traced any further, and appeared to end at the border of the hyaline layer. Whether these were really nerve-fibrillæ or not was impossible to ascertain.

Finally, after all that we have seen, the structural process exhibited in glandular tissue can be defined as a constantly progressive budding; moreover, it should scarcely be questioned that this process depends virtually upon the growth of the epithelium; it is also certain that the tough stroma lying between the ducts gradually dissolves and diminishes precisely in proportion as the ducts advance towards the formation of terminal vesicles; as yet, however, it is scarcely possible to make a histological distinction of the causal relation in these two processes. It is worthy of mention, in addition, that simultaneously with the origin of the glandular vesicles there is an appearance of fat-cells in the stroma. These cells may be regarded as to a certain extent evolved during this process, as a secondary production.

The changes made in the mammary gland during pregnancy, in preparing to assume its proper functions, are first of all apparent in an enlargement of the secreting surface; the vesicles are broader; the same is true also of the ducts; the hyaline limiting membrane is not so thick; in the interior, fat-vesicles appear at first singly and in the midst of cell-masses, finally in such quantities that they fill and considerably dilate the sacculated terminal vesicle, and even press the epithelium entirely to the wall.

Then, too, the interlobular connective tissue becomes gradually looser and is continually enclosing more fat. The tough part of the stroma diminishes though it never entirely disappears, for even in nursing-women a firm kernel can still be felt in the interior of the organ. These occurrences are not simultaneous in all portions of the glands, and even as late as in Women who have died shortly after delivery we still observe many transition-types existing among the elements in the terminal vesicles. It is unquestionable that the fat-corpuscles—anatomical elements of milk—are really derived from the epithelium of the glandular vesicles; for in the first place we have prima facie evidence of the fact, since the primary fat-vesicles appear in the very middle of the epithelial mass; a second proof is the occurrence of globular cells containing nuclei and distended with fat-vesicles (colostrum) in the first milk of Women after delivery; lastly we can sometimes find fat-vesicles in the cells of the acinus, and this is not only true of isolated but also of embedded cells. I have found some cells which contained small fat-drops and others whose nucleus was crescent-shaped and embraced a large fat-drop. The larger fat-globules in parietal cells are situated more towards that extremity of the cell which is directed towards the lumen, but the nucleus is placed nearer the wall. From this it is evident why the walls of empty acini are so frequently filled with fat-vesicles, for the epithelial cells thus distended burst and allow the fat-globules to escape. It is questionable whether the epithelial cell then perishes and is immediately succeeded by another, or whether it survives and is capable of producing new milk-globules. The latter theory is probably the correct one, and is in accordance with the observations of S. Stricker,* who also states that the colostrum-cells, already given off and floating in the fresh milk, supply fat-globules.

Fig. 231.

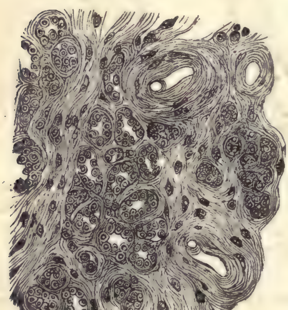

Fig. 231. Terminal vesicles and stroma from the mammary gland of a nurse who died after an illness of three weeks. System No. 8. Hartnack.

Involution of the Parenchyma seems to take place at the moment the gland ceases to be used for suckling. In a nurse that died after an illness of three weeks I found the glandular lobules were already shrunken, compressed, and separated by broad connective-tissue septa as before pregnancy; they contained but little fat. The glandular vesicles had become small and now contained no fat-globules; the epithelial cells were sometimes in irregular heaps, sometimes distributed along the wall: still *injection-masses* could sometimes be forced through the ducts into the terminal vesicles. The largest ducts contained a brownish tough substance in which fat-globules were mingled. The same condition was shown in the mammary gland of a Bitch three weeks after bearing young.

I have also met with this characteristic feature of the glandular paren-

* Wiener akad. Berichte. B. 53. Abth. II. pag. 184.

chyma in a still vigorous Woman who had borne children a considerable time before; it should be regarded, therefore, as the quiescent condition of the organ. In many cases, however, it happens that a still further involution takes place in some portions of the gland, for in the very same Woman alluded to I observed, near some wide ducts, closely-compressed though short buds. In general, small terminal buds and acini, too, when they are connected with dilated ducts, must be regarded as indicating a previous puerperal condition. This much is certain, in healthy, non-enervated Women the glandular vesicles maintain their shape, sometimes remaining as in Virgins, though without the hyaline membrane.

Fig. 232.

Fig. 232. Termination of ducts; the stroma contains some capillaries and an abundance of elastic fibres. From a woman 90 years of age.—System No. 8.

Entire disappearance of the glandular vesicles does not take place until the climacteric years are reached; then the tough fibrous stroma fails completely; the entire gland collapses and constitutes a thin membranous disc, which is attached to the nipple and is enveloped on both sides by adipose tissue. In what remains of glandular substance we find ducts simply; these, however, have delicate little branches, to be regarded as intra-lobular. These last diverticula of the ducts represent what seem to be cylindrical prolongations ending blindly, and have no further appendages; they are generally thin-walled, mostly collapsed, and therefore on transverse section exhibit a cleft opening; the parietes are clothed with a single coat of low epithelium. The ducts, which are now so contracted in size, are held in position by a loose fibrillated connective tissue, interwoven with which is an abundance of elastic fibres. Many fat-cells, too, so arranged in rows as to form little chains, occur in this stroma.

For investigating the coarse duct-structure it is well to employ injected corrosive preparations. Sometimes injection of young glands succeeds so well that we can trace the course of the ducts as far as to the last outrunners. Glands hardened in alcohol, or boiled in pyroligneous acid, make very suitable subjects for studying the budding process in young ducts, as well as their structure and stroma. Pyroligneous acid preparations also furnish a ready means for examining the arrangement of the muscular tissue and papillary bodies in the nipple.

Objects hardened in the bichromate of potash, or absolute alcohol, furnish instructive preparations for examining the epithelium in the terminal vesicles. Staining the sections with carmine displays the more delicate contours of the epithelium, and perosmic acid colors the finest fat-globules in the cells. Sometimes the injection of blood-vessels in glands after removal from the body is successful, if we make use of Herring's apparatus and injection-masses that flow well.

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CHAPTER XXIX.

MALE AND FEMALE EXTERNAL GENITAL ORGANS; TOGETHER WITH THEIR GLANDULAR APPENDAGES.

By E. KLEIN.

Male Organs.—Vas Deferens.

The vas deferens is a structure rich in muscular fibres, and is similar in many respects to the excretory ducts of the larger glandular organs. It consists of a mucous membrane, a muscular coat, and a loose external connective-tissue envelope, the tunica adventitia.

The inner surface of the mucous membrane is clothed with epithelium, which, in Adults, and especially in new-born Children, is subjected to various modifications. In Adults it has generally, at its commencement, a single layer of ciliated cylindrical epithelium. The cells themselves are either conical or cylindrical, have a length of about 0.03 millim., and each is provided with a rounded or oblong nucleus, which contains a distinct nucleolus. It happens sometimes, though rarely, that spindle-shaped cells are inserted between the conical ones, and thus the cylindrical epithelium embraces several sorts. The conical cells are furnished with very short delicate cilia, both where the epithelium has but one layer and where it has several.

The limit at which the cells nearest the outlet lose their vibrating cilia is different; it is not the same for the whole periphery, and my experience would justify me in saying that ciliated cells are certainly no longer visible at four centimetres' distance above the epididymis. In tracing the tube outwards in adult cases, the epithelium continues to exhibit about the same characters, with this difference only, that we can clearly recognize a striated basal border in very many cells. In Children there is a great difference between the epithelium of the extra- and intra-abdominal portion. In the former the epithelium is mostly laminated, and the following order is maintained: the superficial layer is composed of short cylindrical cells, and underlying this are one or two laminæ of the polyhedral or rounded variety. All cells, whether near the outlet or further removed, have a relatively large nucleus, generally rounded. In that portion of the vas deferens, however, which is situated within the abdominal cavity, the structure of the epithelium is similar to that of Adults; we observe here beautiful elongated cells, both conical and cylindrical, with a border of rods.

These cells are sometimes uniform in character, though it more frequently happens that spindle-shaped cells make their way in from outside. In new-born Children the thickness of the epithelium, in those portions of the vas deferens lying without the abdominal cavity, reaches almost 0.02 millim., while the thickness of the corresponding coats within the same cavity measures 0.03 millim. In tracing the vas deferens towards the ampullæ, we observe but a slight increase in the dimensions of the epithelium.

The mucous coat underlying the epithelium is folded in two or three longitudinal rugæ; at and about the ampulla these are still more numerous,

and reach a considerable height. At this point these folds are connected with one another by single little transverse ridges; the fossæ or depressions thus enclosed have been regarded as glands by some investigators (Henle, Leydig).

Connective tissue and elastic fibres are the elements of the mucous coat. The former comprises intersecting bundles of fibres; in the external portions they are usually parallel to the direction of the vas, though they assume a more oblique course as they approach the epithelium, and terminate in ascending and descending fibrils.

The elastic fibres form tolerably close net-works, which are connected externally with the septa of the muscular bundles in the same way as the connective-tissue bundles associated with them. By means of these septa they are still further connected with the looser tunica adventitia. The thickness of the mucous-tissue layer depends on the thickness of the muscular tunic, to which it bears an inverse relation; this latter, with the exception of the commencing-portion of the vas deferens, is composed chiefly of two layers, an inner or circular and an outer or longitudinal muscular layer. The direction of the fibres in these two coats is rectangular one to the other.

Both consist simply of smooth muscular fibres. From the very commencement, as far as to within two centimetres of the epididymis, there is always an internal longitudinal layer; elsewhere this is represented by occasional bundles lying within the circular layers.

In Adults the thickness of this inner longitudinal coat amounts to from 0.06 to 0.1 millim. The thickness of the middle circular coat gradually decreases from the commencement of the vas deferens towards the ampulla.

At the ampulla it again attains its former size. The external muscular coat, too, is more developed at its commencement than in its subsequent course; it measures there about 0.05 millim. The muscular tunics are less developed in new-born Children than in Adults. Finally, wherever an internal longitudinal coat exists, these scattered little bundles of smooth muscular fibres penetrate obliquely and longitudinally into the mucous tissue, and are to be met with quite close under the epithelium. Furthermore, the outermost bundles of the circular layer intersect in many places with the bundles of the longitudinal coat; this relation is very distinctly marked at the ampulla and in its vicinity, for at this point a number of bundles from the external or longitudinal coat press in obliquely between the circular bundles in order to terminate in that tissue.

On one side of the tunica adventitia there are some larger and smaller bundles of smooth muscular fibres running longitudinally; they are grouped in a semicircle about the vas, and are separated from one another by a varying distance. Henle has named them the cremaster internus. In many places these muscular bundles are so closely related to those of the external muscular coat, that it is impossible to separate the two. The cremaster internus is most strongly developed at the commencement of the vas deferens; from this point until it enters the abdominal cavity there is a progressive diminution in thickness, yet the range of its distribution is increased, for we can detect single bundles of smooth fibres running longitudinally throughout the entire periphery of the adventitial tunic. The nerve trunks constitute a pretty dense plexus—the plexus spermaticus—situated in the tunica adventitia, though in a portion distant from the cremaster internus. The nerve fibres of which the trunks consist are medullated throughout. From the sheath connective-tissue cords are usually sent towards the interior of the nerve trunk, separating the nerve-fibres into two

or three bundles. These bundles, perhaps, correspond merely to various sources from which the nerve-trunks derive their origin, for it is well known that the nerves which enter the plexus spermaticus are derived from the spermatic and sympathetic. Issuing out of the plexus spermaticus are several smaller nerve trunks; these penetrate the muscular and mucous layers of the vas deferens where they are observed to have medullated fibres. In the upper portion of the vas deferens small ganglion-cells are scattered in the nerve trunks of this plexus and also in those trunks lying more externally and running separately. In the neighborhood of the ampullæ, however, there are some quite feebly developed ganglion-cells. These latter are rounded or oblong, and are about 0.35 millim. in diameter.

Fig. 233.

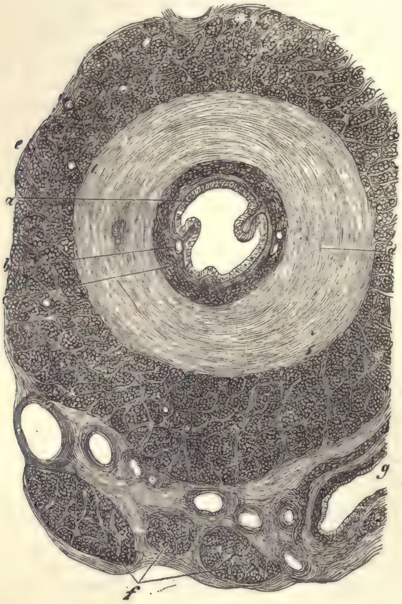

Fig. 233. Transverse section through the commencing portion of the vas deferens; *a*, epithelium; *b*, tunica mucosa; *c*, inner; *d*, middle; *e*, outer muscular layer; *f*, bundles of the cremaster internus; *g*, vein containing muscles in its wall. System No. 2; Ocular No. 3. Hartnack.

The sheath of the ganglionic knot consists of a common fibrillated connective tissue containing occasional spindle-cells. Some of the fibres penetrate from the periphery into the interior of the knot; these are connected with the cell-net spread out through the knots. The ganglion-cells seen here are small and furnished with two or more processes, and the nucleus, which is relatively large, clearly defined, and bright, has also a distinct nucleolus. Each ganglion-cell lies within a nucleated capsule, which, here as elsewhere, is continued as a connective-tissue sheath for the nerve fibres belonging to the cells.

It is only in new-born Children that distinctly nucleated and granular cells are seen in the nodal points of the network, recently described as found in the interior of the ganglion.

Associated with the small ganglion-cells—0.0014 millim. in diameter—observed in the ampulla and more external portions of the vas deferens, there are also numerous ganglion-cells measuring as much as 0.03 millim. Both of these varieties have a nucleated capsule.

On the outer side of the nerve-plexus, which is usually found on but one side of the vas deferens, there is the well-known plexus of veins known as the plexus pampiniformis, besides some arterial vessels of less size. This vascular system is connected with the proper vessels of the vas deferens; the rich capillary network of the muscular tunic, as well as the sub-epithelial network of the mucous layer are worthy of mention. The walls of the smaller veins constituting the pampiniform plexus are remarkable for their thickness, and further for exhibiting three well-marked coats, viz.: an inner, containing elastic fibres and single muscular bundles, running horizontally; a middle, composed chiefly of circular muscular fibres; and, finally,

an outer loosely-knit adventitial tunic containing longitudinal muscular bundles.

In the still more external portion of the spermatic cord, on the side opposite the cremaster internus, we encounter small, smooth muscular fibres running horizontally and combining to form a layer. These bands might appropriately be embraced under the name of Cremaster medius. The spermatic cord is rich in thin-walled broad lymph-vessels; they form distinct networks in the vascular and nerve layer; some of them, too, can be recognized quite close to the muscular coat of the vas deferens.

Besides the structures above enumerated there is a body situated in the commencing portion of the spermatic cord, which is known by the name of parepididymis, or Giraldès's organ. It is entirely made up of canals. These canals are clothed with a cylindrical epithelium similar in every respect to the epithelium of the vas deferens. The mucous membrane underlying the cells is loose, very rich in folds, which in some places have the appearance of glandular cavities. The mucous membrane, as usual, contains a meshwork of connective tissue and elastic fibres. On all sides we encounter small circular bundles of smooth muscular fibres.

Externally the mucous membrane is surrounded by a pretty dense network of veins.

A vas deferens exists in all Mammals, Birds, scaly Reptiles and Selachians, and always has a definite muscular character. According to Leydig the vas deferens of Mammals in its lower and dilated extremity—the ampulla—is rich in glands, while the vas deferens of Birds, Saurians and Snakes is entirely without them. It is probable, however, that Leydig makes the same error here as in the case of Man and regards the lacunar depressions of the mucous membrane, in the animals just enumerated, as true glands. It has also been observed that smooth muscular fibres exist in the lower portion of the common urino-seminal duct of Batrachians.

Seminal Vesicles.

In these structures we recognize, with slight modifications, almost all the elements that belong to the vas deferens. The mucous membrane is folded into rugæ of varying height, and these folds are not always parallel to the

Fig. 234.

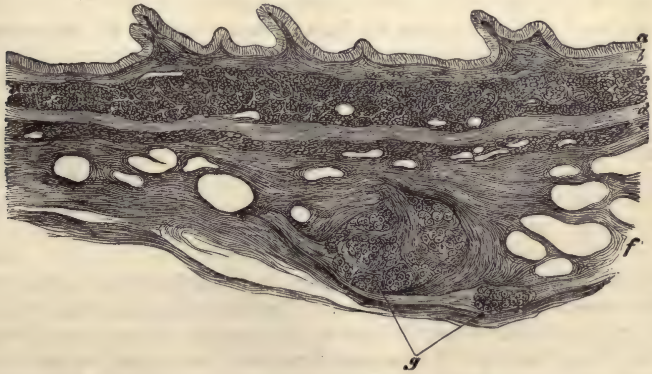

Fig. 234. Transverse section through the wall of a seminal vesicle. *a*, epithelium; *b*, mucous layer; *c*, internal, *d*, middle, and *e*, outer muscular coat; *f*, adventitial tunic; *g*, ganglia. From a Child. System No. 4. Ocular No. 3. Hartnack.

axis of the canal, for there are also, at intervals, prominent transverse ridges. This latter circumstance explains the origin of the lacunar depressions which Henle describes and calls glands. As in the vas deferens, so here, the epithelium is cylindrical; the conical or cylindrical cells composing this layer are furnished with a well-marked outer border of rods, which, in new-born Children especially, gives exactly the appearance of short fine cilia.

The mucous membrane, including even the folds, is furnished throughout with small muscular bands. The thickness of this tissue reaches 0.04 millim.

The muscular coats usually consist of three layers, an internal or longitudinal, a middle or circular, and an external or longitudinal. The inner is the strongest; the middle and external have about the same thickness; in new-born Children the thickness of the inner and middle coat is 0.12 millim., that of the external is 0.03 millim. An adventitial tunic, amply supplied with networks of vessels and nerves, lies outside of the muscular. The ganglionic knots inserted in the nerve-plexus attain their highest development in the seminal vesicles. Here they contain large ganglion cells, usually having a single nucleus, though occasionally two. Leydig states that the seminal vesicles in Mammals are glandular apparatuses, and he further adds that they are either provided with groups of racemose glands closely crowded together, or assume the type of a single gland of that character.

Ejaculatory Ducts.

We distinguish in the ducts a cylindrical epithelium, 0.014 millim. high, which is composed of one layer in the first portion. The nearer the ducts approach the vesicula prostatica (sinus pocularis) the more sudden is the change from the cylindrical epithelium already mentioned, to a transitional form; we find beneath a superficial layer, consisting of short cylindrical or club-shaped cells, still smaller cells, nearly polyhedral or but slightly elongated. The laminated pavement epithelium characterizing the vesicula prostatica is continued a short distance into the orifice of the duct. Here also the surface of the mucous membrane is uneven and marked with prominent longitudinal and transverse folds; these latter increase in number and size almost up to the orifice of the ejaculatory ducts. The mucous membrane is 0.06 millim. in thickness, and consists of connective tissue, of which the greater part is devoted to forming a network parallel to the axis of the duct. There are also bundles, composed of smooth muscular tissue, which pursue a similar direction. Exterior to the mucous membrane is a circular muscular coat 0.06 millim. in thickness. This latter is continued over the ejaculatory duct into the circular muscular tunic of the vesicula prostatica, to be mentioned in another place.

Prostate.

In this organ we distinguish structurally two entirely distinct elements, viz., a glandular and a muscular substance. The latter, as Kölliker has demonstrated, constitutes the proper stroma of the prostate, since the connective tissue which forms the septa for the muscles as well as a framework for the vessels and nerves, is represented by only very slight trabeculæ, and they penetrate the interior of the prostate from without. Externally, this organ possesses a connective-tissue envelope which is in direct connection with the

tendons of the smooth muscular bands adjacent to it. These latter have a circular or oblique course; there are also some intervening muscular bundles which pursue a straight course. These muscular masses constitute the proper cortical substance of the prostate. Pressing inwards from this muscular cortex stout muscular cords reach the interior, forming a trellis-work as they proceed. The interspaces thus formed serve for the reception of the gland substance. The thickness of the cortex just described varies according to its position, viz.: whether before or behind the urethra; it differs further in the upper, middle, and lower portions; for while the portion lying in front of the urethra consists almost entirely of cortical substance—that is, muscular tissue mostly—the cortical substance along the posterior periphery of the organ is comparatively stouter in the upper portions than in the middle, and in the middle than in the under. From this explanation it is evident that the glandular substance is comparatively most highly developed behind the urethra and in the lower portions, and that it is only feebly represented in the part anterior to the urethra. The form of arrangement assumed by the glandular substance depends very greatly upon the character of the muscular trabeculæ penetrating the interior of the organ. In the lower sections of the prostate, lying behind the urethra, the muscular bands form a loose, broad-meshed texture; this portion of the prostate, therefore, has somewhat the appearance of a spongy mass.

In the middle portions the muscular bands constitute a true envelope for the central portions of the glandular substance, for it encloses this semi-circular, uniformly dense mass and is the source from which the delicate fasciculi are derived which press in between the glands. Finally, in the upper portion the muscular bands are quite unequally and irregularly distributed. These statements explain why we find in those portions of the prostate lying behind the urethra, superiorly, a more compact tissue, while lower down the substance is tolerably uniform, and below represents a spongy glandular mass. In Adults the middle portions measure 6.6 millim.

As to the structure of the glands themselves, we find ourselves dealing with those of the so-called acinose variety; that is to say, with glandular ducts whose basement membrane is structureless. These, after pursuing a slightly tortuous course, subdivide into two or more smaller ducts, which are provided with lateral and terminal diverticles of various lengths, spherical or ovoid in shape. The wall is always structureless. In the central section of the gland the smaller passages leading into the principal excretory duct are provided with semicircular diverticles—acini.

In the lower portion of the prostate we discover almost nothing but very tortuous tubes, which give off numerous branches, exhibit numerous large varicosities, and at the extreme ends run a remarkably spiral course.

The glandular vesicles and ducts are generally invested with a single layer of cylindrical epithelium 0.026 millim. in thickness; there are places, however, as, for example, in the lower spongy glandular substance, where the epithelium is shorter and cubical; in this latter case there is an additional row of smaller rounded cells beneath them upon the basement membrane.

The cells, individually, are cylindrical or conical; the nucleus is rounded, and lies almost invariably in the outer third of the cell. In the smaller excretory ducts there is, at intervals, beneath the usual layer a deeper one of small rounded cells, which are distinguished by having proportionately large nuclei; there are also spindle cells embedded between the outer extremities of the most superficial layer of cells. These latter cells furnish a special proof of direct connection between the process of one cell and the contiguous tissue.

The nearer the glandular excretory ducts approach to their orifices the narrower they become, and the greater the change in the cylindrical epithelium. At the base of the caput gallinaginis—at the orifice of the broad excretory ducts of the central glandular substance—those passages that have a diameter of 0.31 millim. are paved with the transitional epithelium of the urethra for a short distance inwards; sometimes, however, when the mouths of these ducts measure 0.13 millim. they are invested with pavement epithelium, and the neighboring portions of the passage receive a partial covering of the same nature.

Fig. 235.

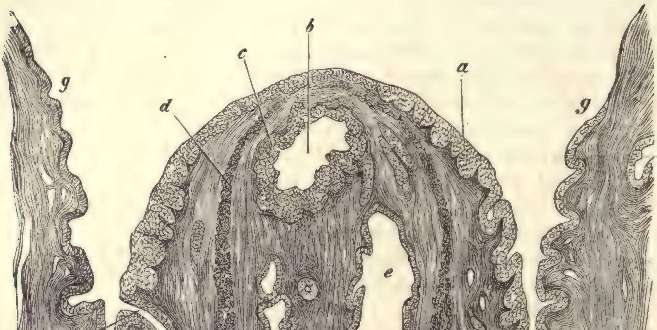

Fig. 235. Transverse section through the caput gallinaginis. *a*, epithelium of surface; *b*, vesicula prostatica; *c*, epithelium of the vesicula; *d*, muscles; *e*, ejaculatory duct; *f*, excretory duct of the prostatic glands; *g*, upper wall of the urethra; muscles running vertically. From a Child. System No. 2; Ocular No. 3. Hartnack.

The excretory ducts of the prostatic glands, lying not much anterior to the urethra, as well as excretory ducts of the upper and lower glands, lying behind the uretha, and especially of those opening through the lateral urethral wall, are clothed at the orifices with laminated pavement epithelium, or not uncommonly with laminæ of the transitional variety.

Transversely-striped muscles occur in the prostate as connected bands, internal to the transversely-striped fibres of the sphincter urethræ.

Henle described such circular bands in the superior part of that portion lying in front of the urethra; yet they extend further downward, reaching into the cortical layer, as Kölliker has shown. In the cortical substance of that portion lying behind the urethra there are also bundles of transversely-striated muscular fibres; these are mostly found in the upper part, where, in company with bands of smooth muscular fibres, they press in between the gland substance to the interior.

Fig. 236.

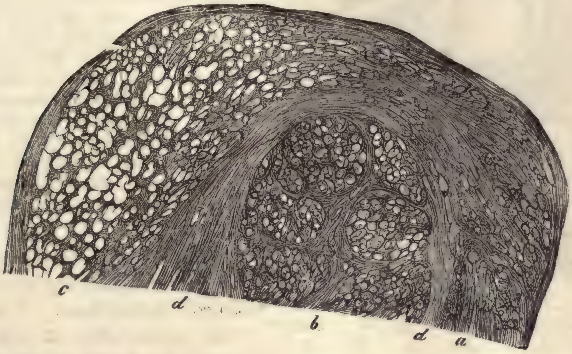

Fig. 236. Longitudinal section through that portion of the prostate lying behind the urethra; *a*, compact; *b*, central; *c*, spongy gland-substance; *d*, muscular envelope of the central part. From an Adult, magnified 3 diameters.

The tunica adventitia is formed of loose connective tissue containing fat, and sustains dense networks of vessels and nerves, especially in the posterior portions.

Large trunks, derived from the vessels surrounding the prostate, press into the interior of the organ, and constitute a broad-meshed capillary system about the glands. In the caput gallinaginis some large vessels approach quite near to the urethra, and then become capillary; the veins derived from these capillaries are connected with the veins of the urethra.

Nerve trunks composed of medullated fibres surround the cortex; they are everywhere interspersed with numerous large ganglion-cells, or are connected with oval ganglionic knots. These latter are less numerous here than in the seminal vesicles; their diameter reaches 0.53 millim. J. Müller was one of the first who observed ganglions on the sympathetic nerves at the side of the prostate.

Pacinian bodies are also found in the cortical substance of the prostate. In the interior are very numerous small trunks of medullated fibres, which form nets in all directions. A very large number of nerve trunks pursue a vertical course between the Sphincter urethræ and the circular, transversely-striated muscular fibres of the cortical layer, where they ascend quite to the urethra. These contain a chain of ganglion cells interspersed between their fibres.

In many gland-ducts and vesicles flakes of a yellowish or brownish color occur, and are to be regarded as the secretion of the glandular epithelia; the mode of their formation can be very accurately studied here, just as in the thymus gland. Both in the cortical and glandular substance there are yellow and brown pigment-flakes, and spindle cells bearing pigment granules.

In the upper and posterior portion of the prostate there is a remarkable organ. It has somewhat the appearance of a large duct, yet the wall is like that of an artery; in other words, it consists of an internal longitudinal, a middle circular, and an external longitudinal tunic. The middle layer consists mostly of smooth muscular fibres, while the internal and external are only in part composed of them. The interior of this structure is filled with numerous small vascular nets, pigment flakes, and cords of smooth muscular fibres.

Fig. 237.

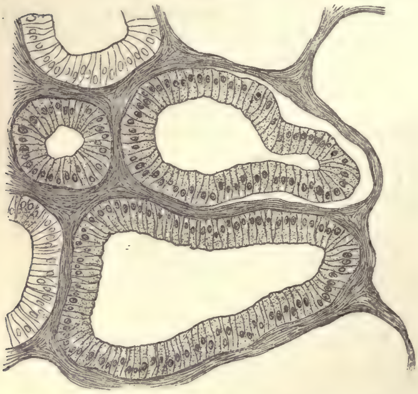

Fig. 237. Transverse section through the central granular substance of the prostate. From an Adult. System No. 5, Ocular No. 3. Hartnack.

The prostate is common to all Mammals, while Birds have no analogue that we know of; in tailed Batrachians the pelvic and rectal glands which discharge into the cloaca and become tumid during copulation might be regarded as corresponding to Cowper's glands and those of the prostate. Similar organs occur in the cloaca of the Saurians. Fish have agglomerations of vesicles which communicate by canals with the vas deferens. (Leydig.)

The caput gallinaginis is clothed with a beautifully laminated pavement epithelium. This serves at the same time as the epithelium proper of the lower wall of the urethra. Its thickness is materially greater at the base than at the orifice. In the former position it measures 0.31 millim., in the latter only one-third as much; we observe at the base of the caput conical and vascular papillæ, which are enlarged at the apex and project into the epithelium. They diminish in height as they approach the orifice, and at that point are rarely met with.

The vesicula prostatica, too, is invested with a laminated pavement epithelium, into which small, conical papillæ project. Both in the caput and sinus pocularis, there are little glands opening upon the free surface; these are short, branched, and tortuous, and lined for a short distance inwards with the laminated pavement epithelium of the urethra.

The vesicula prostatica is traversed by a small amount of connective tissue—the framework for vessels—and by an abundance of muscular fibres. The latter are connected with the smooth muscular fibres stretching upwards from the interior of the prostate, as well as with those which exist in the wall of the ejaculatory ducts. In general, it may be said that the bundles lying nearest the prostatic vesicle intercross one with the other obliquely.

Upon these oblique fibres there follows a layer of circular ones, which are to be regarded as direct continuations of the external circular-muscle layer of the duct. This circular envelope of the vesicula prostatica attains its minimum of development in the neighborhood of the epithelium of the caput gallinaginis.

Urethra.

A laminated pavement epithelium covers the inferior wall of the urethra, at the root and in the prostatic and membranous portions; the sides and superior wall of these parts are mostly lined with layers of transitional epithelium, in which some small islets of the laminated pavement variety occur.

There is, however, a diversity in the forms of the transitional epithelium,

and club-shaped cells are observed in the middle layers, while in the upper ones there is a combination of the pavement and club-shaped variety. The thickness of the epithelium varies between 0.09 and 0.1 millim., and is somewhat less on the upper than on the lower wall.

The mucous membrane, which in thickness bears an inverse relation to the muscular tunic, and averages from 0.36 to 0.45 millim., is structurally different in Children and Adults.

This membrane in Children, as well as the septa of the muscular tunic with which it is united, consists of a very delicate homogeneous network. The nodal points in new-born Children frequently contain distinctly nucleated cells, which latter are mutually connected by short, thick processes, and form connections, too, on all sides with the tunica adventitia of the coarser and finer vessels. Besides, in this network there are such trabeculæ as represent a bundle of fine connective-tissue fibrillæ, so that it is not improbable that the cell-processes of these adenoid meshworks break up into fibrillæ and so constitute the connective-tissue bundles. In Adults we actually find nothing but networks composed of intersecting bundles of connective tissue, together with nets of elastic fibres.

From the surface of the mucous membrane numerous small conical papillæ press into the epithelium; they are shorter, and occur less often on the superior and lateral walls than on the inferior.

Further, glands are to be met with in the mucous membrane. These are branched tubes, furnished with two or more diverticles. They are enclosed by a structureless wall; in the diverticles, and those other portions of the tubes lying deep down in the mucous membrane, a single lamina of cylindrical epithelium is to be met with; nearer the orifice the tubes are invested with a laminated transitional epithelium, and at the orifice itself with laminæ of the pavement order.

These glands—Littre's glands of the urethra—occur both in the prostatic portion, on the lower and lateral wall, and also in the membranous portion; in this latter situation single examples, sunk at varying depths in the mucous membrane, may be met with at any point in the periphery. Some of the glands lie between the great venous plexuses, and are surrounded by smooth muscular fibres, and others extend inwards as far as the muscular tunic.

At the base of the urethra this muscular coat has two layers, viz., an internal circular and an external longitudinal layer of smooth fibres. In the lower portion the circular coat consists almost solely of small bundles, separated from one another by an abundance of connective tissue; the thickness of this layer in Children measures from 1.3 to 1.6 millim. The external lamina is somewhat weaker and consists, too, solely of smaller fascicles. Both coats are mutually connected by intersecting bundles having an oblique course; and in approaching the upper extremity of this portion of the urethra, the texture of both the inner and outer muscular tunic becomes somewhat denser; the bundles become larger, and consequently are proportionately nearer together. Throughout the entire circumference, small fasciculi are observed to press obliquely into the mucous coat, where they break up into single fibres and are to be traced quite up to the epithelium.

In the prostatic portion the muscular tissue of the urethra has an intimate connection with that of the prostate; it is observed to consist mostly of bundles of smooth fibres having a longitudinal direction and situated close to the mucous membrane. In the same portion it is impossible to discover more than one longitudinal muscular layer contiguous to the mucous membrane; this is about 0.58 millim. thick, and solid, sending off numer-

ous bundles, which diverge in an oblique direction to penetrate the mucous membrane.

The large vascular and nervous trunks lie outside of the muscular tunic; the arteries, after furnishing numerous branches for this substance, penetrate the mucous tissue, and end in the sub-epithelial venous capillaries of the papillæ as single and double capillary loops. These vessels, increasing rapidly in size, and communicating with one another by numerous anastomoses, constitute a venous plexus proper for the mucous membrane, the general direction of which is parallel to the urethra. Muscular bands, derived from the muscular coat, press in between these large veins. The thickness of the network gradually increases towards the anterior end of the pars membranacea.

The venous branches passing outwards suffer a further diminution in size and number, or in other words smaller venous vessels penetrate outwardly, and in their passage through the muscular tunic take up veins of the latter.

From this explanation it becomes evident that with an increased influx of blood to the arteries of the urethra the reflux through the returning veins cannot be proportionate, and that stasis of the surplus blood in the large venous networks must result. It is further clear, too, that the network of the mucous membrane described above is cavernous, and that we must agree with Henle in regarding this portion of the urethra as having a cavernous body, though but feebly developed.

The nerves exhibit here the same characteristics as we have observed elsewhere outside the muscular tunic. Ganglionic knots are interspersed throughout those nerve-branches which are composed of medullated fibres.

Lovén found ganglionic cells and ganglionic knots in three places: first, in the posterior surface of the membranous portion; second, in the dense connective tissue at the posterior portion of the bulb, and lastly in the networks which the lateral trunks of the nervi erigentes form about the vessels at the side of the bulb.

Previous to the enlargement of the corpus cavernosum urethræ * into the bulb, and near the point where the crura penis meet the urethra (which still lies below them), we observe pushing upwards between the two ischio-cavernous and perineal muscles a mass of smooth longitudinal muscular fibres. These are grouped in bundles of varying size, and when seen in cross-section are found to be distributed over a circular area whose diameter is 2.25 millim. In the central part of the mass the bundles are more closely packed together than in the peripheral. On the upper or urethral side some oblique or even nearly circular bundles are seen. In direct connection with the muscular mass is a layer of longitudinal smooth muscular fibres, which is situated between the Cowperian glands and their excretory ducts, or, more properly, the crura of the penis. This muscular mass is only separated from the excretory ducts of the Cowperian glands by a layer of smooth muscular fibres running parallel to the course of these ducts. The thickness of this muscular layer between the Cowperian glands reaches 0.89 millim.; that between the crura of the penis 0.54 millim. Numerous bundles diverge from this muscular mass and press in between the lobules of Cowper's glands, where they terminate. Transversely striated muscles—the ischio-cavernous and perineal—reach the same points after penetrating the glands from without and below.

The muscular layer mentioned above is also connected with the muscular trabeculæ of the crura penis: it ascends, becomes narrower while pointed above and below, and terminates in a connective-tissue partition-wall which

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* Seu corpus spongiosum urethræ.—TRANSLATOR'S NOTE.

is in direct communication with the bundles of connective tissue lying in the under surface of the corpus cavernosum urethræ.

A lamina of longitudinal muscular fibres, 0.54 millim. in thickness, approaches the septum from either side, meeting it at an obtuse angle; it is a direct continuation of the muscular tunic of the urethra, encircles the corpus cavernosum of the same name, with whose muscular trabeculæ it is connected. At the point where the muscular layer on either side is arrested at the septum, just mentioned, there are several large venous trunks rising vertically from the corpus cavernosum of the crura penis and penetrating into the erectile body of the urethra.

A description of Cowper's glands may be appropriately introduced in this place:—

The position they occupy has already been noticed; we will now study their structures. These bodies are oblong, and their long axis is directed obliquely inwards and downwards. The duct of each gland ascends near the crura of the penis, and in this situation is 0.18 millim. in width, lined with cylindrical epithelium, and, as previously mentioned, is accompanied by a layer of smooth muscular fibres, running parallel to the longitudinal axis. It diminishes in width as it approaches its orifice. From each gland are given off a large number of branches, which are furnished with two or more dilatations whose diameters are from 0.08 to 0.12 millim.; these are the acini. The epithelium is cylindrical and the basement membrane structureless.

The glandular substance is surrounded here as elsewhere by a tolerably dense capillary network.

The fibrillar portion, in which the glandular substance is embedded, consists mostly of muscles,—as already stated,—though connective tissue is intermingled to a slight degree.

In the vicinity of the bulb the mucous membrane of the entire lower and greater portion of the lateral surfaces of the urethra exhibits laminæ of pavement epithelium 0.18 millim. in thickness. In this respect it is similar to pavement epithelium of the buccal cavity and other places, with this exception, that the uppermost cells do not seem to be so much flattened, and some bear an oblong nucleus and others a roundish one. The cells of the deepest layer are cuboidal or polyhedral, and have also a rounded and proportionately large nucleus. From the bulb onwards the laminated epithelium gradually diminishes, existing only for a short distance in the median line of the under surface. It is at first succeeded by a laminated transitional epithelium, and finally by the cylindrical. Upon the sides, and especially on the upper surface, this change occurs earlier. Yet in this respect variations are observed, for in new-born Children it is not unusual to find islets of laminated pavement epithelium on the upper as well as under surface. The cylindrical epithelium, with which the urethra is lined until quite near the fossa navicularis, exhibits an upper layer of true cylindrical cells, but nearer the basement membrane cells of the club or spindle-shaped order. Yet there are places where but a single tunic of the cylindrical variety exists. At the point where the course of the urethra commences to be straight from behind forwards only pavement epithelium is found. The posterior portion of this coat is materially thicker than the anterior. There is a further difference between the epithelium of this anterior and posterior half of the penis, for in the former the uppermost cells exhibit a greater flattening and more thorough coalescence than in the latter. The deepest epithelial layer is always composed of short cylindrical cells, which are placed close together like the timbers of a stockade—each cell having a rounded nucleus. The mucous mem-

brane of the urethra is marked throughout its whole length by longitudinal folds, which also appear connected in places by horizontal ridges. It is in this way the Lacunæ Morgagni are formed.

The thickness of the mucous membrane is extremely uncertain, since its external boundary cannot be definitely determined. This is explained by the fact that the vessels and muscles of the corpus cavernosum are continuous with those of the mucous membrane. At the root of the penis this membrane attains a thickness of about 0.178 millim., but further forward it is somewhat thinner and then measures about 0.13 millim.

Fig. 238.

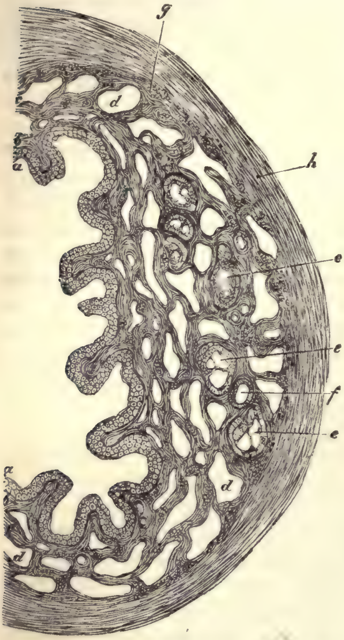

Fig. 238. Transverse section through the spongy portion of the urethra (corpus cavernosum urethræ). *a*, epithelium; *b*, tunica mucosa; *c*, muscular cords; *d*, vascular spaces of the corp. cavern.; *e*, glands; *f*, excretory duct of gland; *g*, longitudinal muscles; *h*, tunica albuginea. System No. 2. Ocular No. 3. Hartnack.

The papillæ, which reach from the mucous membrane into the epithelium, are only numerous and well developed where they are brought in connection with the laminated pavement cells; at the points where a transitional epithelium exists, the papillæ are short and few in number. They are longest along the lower wall of the fossa navicularis and so onwards to the orificium urethræ, where they attain a height of 0.14 millim. All the papillæ of the urethra have a vascular supply; in some instances but a single vascular loop is observed; in others, several loops, as in the fossa navicularis. Wherever papillæ do not exist, or where the mucous membrane is furnished with cylindrical epithelium, we find, as a substitute for the former arrangement, a dense capillary network in the plane underlying and parallel to the epithelial tunic.

This membrane is loose in texture and is comprised of a delicate meshwork of connective tissue, interwoven throughout with separate little bundles of smooth muscular fibres. These latter have a longitudinal or oblique direction, and are continuous with the muscular trabeculæ of the corpus cavernosum urethræ.

Littre's mucous glands have a pretty general distribution, and it is observed that they are more frequently met with on the upper than lower wall. They are broad, tortuous ducts, 0.13 millim. in diameter, which pierce through the mucous membrane in an oblique course forwards. The epithelium of the urethral surface is continued a short distance into the duct. These tubes have the character of solitary glands until they reach the deepest portion of the corpus cavernosum; at this point they are provided with four or five half-spherical lobules—acini—which have a diameter of from 0.08–0.12 millim., and not infrequently lie close to the albugineous tunic of the cavernous body.

A single layer of cylindrical epithelium lines the greater portion of the excretory duct and acinus. In new-born Children the nucleus of the cells

is not rounded in every instance, but, as in Adults, flattened, and the long axis is vertical to that of the cell, which latter is near to the membrana propria.

Since the greater portion of each gland is always embedded between the vessels of the corpus cavernosum and is also invested by muscles, it is quite evident that erection of the virile organ can exercise a material influence upon the discharge of secretions. It is possible, too, that it may influence the secretion itself.

Finally, lymphatic vessels are pretty frequently met with in the urethra; their position is in the mucous membrane near the epithelium; their course is parallel to the passage, and they are connected with one another by transverse and obliquely communicating paths. On the lower wall of the fossa navicularis they are most highly developed.

Penis.

Both in the corpus cavernosum urethræ and in the corpora cavernosa penis the tunica albuginea is chiefly composed of connective-tissue and elastic fibres, though muscular tissue is also found in some portions. The fibres of this tunic are grouped in spiral bundles running parallel to one another, and therefore bear some resemblance to the tissue of tendons. These connective-tissue bands unite in constituting about the corpus cavernosum urethræ a circular coat which is outwardly connected with the loose subcutaneous reticulated tissue.

The erectile bodies of the penis have also two investing coverings; an outer or longitudinal and an inner or circular. The former, however, is only met with at the upper and lateral periphery of the erectile body, while the circular layer is continued along the under surface, and is continued as the median septum between both bodies.

In new-born Children the thickness of the outer or longitudinal layer at the root of the penis measures 0.31 millim., while the inner layer is 0.49 millim. In the shaft of the penis this relation is reversed, for here the outer layer measures 0.45 millim. and the inner 0.26 millim. in thickness.

Numerous spindle-cells are interspersed between the connective-tissue bundles. The elastic tissue assumes the form of close networks both in the albugineous tunic of the corpora cavernosa penis and in that of the corpus spongiosum urethræ. In new-born Children oblong nuclei are embedded in these meshworks.

But there are also other reticula in new-born Children, both in the tunica albuginea of the corpora cavernosa, and also in that of the surrounding loose tissue. These are nucleated cells, which sometimes occur in nets of various extent and exhibit precisely the same characters as have been observed in embryonic tendon-tissue.

Both in the tunica albuginea of the corpus cavernosum urethræ and also in that of the corpora cavernosa penis, especially in the shaft, smooth muscular fibres exist. Their number is larger in the tunica albuginea of the corpus cavernosum urethræ, in which they have a circular course, than in that of the corpora cavernosa penis. In this latter they observe a direction corresponding with the tissue in which they are situated, but the fibres are always circular, where the tunica albuginea has but one layer. Now and then the fibres are grouped together and penetrate obliquely the muscular trabeculæ of the corpora cavernosa.

In the loose tissue lying contiguous to the tunica albuginea large nervous trunks, composed of medullated fibres, are met with. In new-born Children

very many of them, accompanied by smaller blood-vessels, lie quite close to the tunica albuginea, in oblong spaces filled with lymph corpuscles and bounded by connective tissue. These spaces may be regarded as belonging to the lymphatic system. Now, from these nerve-trunks, lying outside of the tunica albuginea, small branches enter the corpora cavernosa, where they are traced for a distance as medullated and further on as non-medullated fibres. They are chiefly derived from the plexus cavernosus of the sympathetic, though to a slight extent also from the internal pudic, whose chief function is to supply the skin as well as the mucous membrane of the urethra.

In the loose tissue that surrounds the albugineous tunic there are groups of fat-cells and Pacinian corpuscles. The latter are to be met with both at the root, in the shaft, and vicinity of the corona glandis. They have been observed by Schweigger-Seidel at a distance averaging between 8 and 10 millim. from the posterior border of the glans. They are all of them elliptical, and the long diameter is parallel to the shaft of the penis. The axis-cylinder, which is very broad, remains undivided at the apex. I have observed these bodies also in the corpus cavernosum of the crura penis.

The muscular bundles about the corpus cavernosum penis unite in forming an outer longitudinal sheath adjoining the tunica albuginea and reaching a thickness of 0.09 millim. There are also oblique bundles establishing a connection between this outer layer and the underlying muscular framework. In the corpus cavernosum urethræ this outer sheath is observed only at irregular intervals and is always feebly developed; in the corpora cavernosa penis, too, it is only met with as an especial sheath in the posterior and lateral surfaces. The muscular cords which are spread out between the vascular spaces, and which the latter bound, consist partly of longitudinal, partly of oblique, and partly of circular fibres, all of which intercross in various directions.

The individual muscular fibres are extremely short in proportion to their nuclei, so that in almost all instances where we observe polyhedral outlines —corresponding to the contours of the cells, in bundles cut transversely across—we also have transverse sections of the nuclei.

The blood-vessels of the corpora cavernosa are arteries, veins, capillaries, and finally a dense network of large spaces, bounded by muscular cords and lined with laminated epithelium; these latter constitute the cavernous substance proper.

The corpus cavernosum urethræ is more complete in structure along the lower wall than on the upper. In the latter the large cavernous spaces extend quite to the albugineous tunic, while on the lower and partly on the lateral wall there is an almost continuous muscular lamina situated between a cortico-vascular layer and the chief bulk of the corpus. This lamina is pierced at some few points for the transmission of vessels passing inwards. A similar arrangement exists in the corpus cavernosum of the penis: the largest spaces are in the centre, but within the limits of a semicircle outwards towards the periphery a continued decrease in size takes place. More externally these spaces or lacunæ are gradually compressed by a sheath consisting almost solely of muscles, and, finally, at the very border of the albugineous tunic, they constitute a feeble cortical layer.

From the centre of each body, in a direction towards the septum, the spaces decrease slightly in size. Those adjacent to the septum of both bodies are mutually connected by oblique and transverse anastomoses, and the transverse branches are accompanied by muscular cords.

From the corona glandis onward towards the anterior extremity of the penis the corpus cavernosum urethræ diminishes gradually in size, the change taking place at first in the upper, and, finally, in the lower wall. There still

remain, however, in the latter some few transverse branches, which unite the vascular spaces of both lateral walls. By and by a connective-tissue partition wall—corresponding to the frænulum præputii—is seen in the lower wall; it enters from without, so that the anterior end of this body appears divided, from below upwards, into two sections. It is observed sometimes that such connective-tissue masses can constitute a true albugineous tunic, circumscribing an elliptical domain on either side of the corpus cavernosum urethræ. At either side within this substance, therefore, there can be, apparently, other cavernous bodies. Now, as soon as the corpora cavernosa penis have tapered down to a point at the corona glandis, the corpus cavernosum urethræ gradually loses its individuality and becomes the corpus cavernosum of the glans. This latter appears open on the under side, and in the vicinity of the urethral orifice is separated by connective tissue into two halves; these are united at intervals by transverse anastomoses. The lack of continuity in the lower wall of the corpus cavernosum glandis is caused by connective-tissue bands which extend upward from the urethra.

In the glans there are fewer muscles in the trabecular tissue between the vessels than in the erectile bodies of the penis and urethra. In the cavernous body of the glans the largest vascular spaces are grouped more closely together in the lower and external portions, while, on the other hand, in the upper portions the spaces are smaller and less numerous. Between and connected with them a close and fine vascular network is spread out, of which mention will be made further on; this delicate vascular net attains a high development in the lower lateral portions.

The vessels which are supplied to the prepuce are directly connected with the cortical section of the lower cleft portion of the glans. As regards the arteries of the penis, they are, as is well known, branches of the common pudic artery. Kobelt has named them the artery of the bulb, the bulbo-urethral, the dorsal and profunda arteries. The latter is the source of the arteria bulbosa penis, which is supplied to the root of the penis and, arching over, anostomoses with its fellow of the opposite side. From this arch the arteria cavernosa penis is given off to supply the corpus cavernosum as far as its anterior extremity. The arteria dorsalis penis furnishes the principal vascular supply for the glans, and contributes twigs, too, for the corpus cavernosum penis.

According to Jarjavay and Sappey, five to eight branches are given off from the dorsal artery; they surround the penis, anastomose with the bulbo-urethral, and terminate in the cavernous body of the urethra. According to Langer, four or five perforating branches must be added to the foregoing; these anastomose with the branches both of the dorsal and bulbo-urethral arteries. But he also adds to these latter the perforating arteries of the arterial septum; they are derived from the arteria cavernosa penis, ascend near the septum towards the vena dorsalis penis, anastomose with one another and, together with branches of the arteria dorsalis penis, with which they communicate, supply the tunica albuginea of the corpora cavernosa.

It is well known that Johann Müller classified the arteries of the corpus cavernosum as nutrient and helicine arteries. (Rami nutritii et arteriæ helicinæ.)

The former, therefore, according to his division, indicate the arteries of the trabecular tissue—or the vasa vasorum—which, after anastomosing freely with one another, terminate in capillaries. He estimated the length of the helicine arteries at one line, and their breadth at one-fifth of a millimetre, and stated that they project into the cavernous spaces in the form of tendrils, do not branch, and terminate abruptly in club-shaped processes which are bent

like horns. He further supposed that at the commencement of the act of erection their extremities open, and in this way fill the caverns with arterial blood. Now, the existence of such arteries is corroborated by some investigators, as, for example, Krause, Kobelt, Hyrtl, Gerlach, and denied by others, as M. J. Weber, Arnold, Segond, Kohlrausch, Rouget; Langer, however, has finally set the matter at rest, after a comprehensive and thoroughly correct exhibition of the facts, and has decided in favor of the latter histologists.

Langer, Valentin, Arnold, and Henle have demonstrated that the greater portion of the helicine arteries are nothing more than the overlapping trunks of arterial loops more or less completely injected; they have shown that the apparent existence of these arteries is due, further, to the form of the muscular trabeculæ, since in those laminæ, in the shaft of the penis, which are cylindrical or have funnel-shaped convolutions, the arterial twigs are unbranched, whereas, in the cord-like trabeculæ, that also are found in the shaft, the vessels are branched, and the so-called arteriæ helicinæ are thus produced. It must be maintained, therefore, with Langer, that all the subdivisions of the arteria corporis cavernosi are essentially of like importance. As to the mode in which the circulation in the corpus cavernosum penis terminates, J. Müller and Krause asserted that arterial blood emptied directly from the helicine arteries into the caverns. According to Valentin, however, the smallest arteries open by funnel-shaped terminations into the venous spaces; Rouget states that these spaces are derived from the arteries of the trabeculæ after opening by slits at the surface of the latter. Langer has shown that there is a different mode of termination in the cortical and central portion of the corpus cavernosum penis; in the former portion small arterial twigs—not capillaries, though requiring a magnifying power of from 15 to 20 diameters to render them apparent—pass over into the coarser cortical layer; near by, at the periphery, is also a transitional form in communication with real capillaries, which latter constitute the finer capillary network of the cortex. In the interior of the erectile body there is also some intercommunication by capillaries. The entire periphery of the erectile body serves as a reservoir through which arterial blood reaches the erectile labyrinth. Further, there are transitions from arterial branches to large veins in the interior of this body, under the form of conical enlargements, which represent a part of the internal venous plexus.

Accordingly, there are three modes of vascular transition in the corpus cavernosum penis. First, there is a direct communication between the larger arterial and larger venous branches. Second, the coarser cortical network of veins receives the finest arterial branchlets. Finally, there is a direct anastomosis between capillaries, as in the finer cortical networks, and in the interior of the erectile body. The erectile labyrinth of the penis is a true venous network. The veins returning blood from the erectile bodies of the penis are the dorsal veins—venæ emissariæ of J. Müller—which contribute to supply the vena dorsalis and the veins on the abdominal side of the penis—venæ emissariæ of Kohlrausch. The former proceed directly from the cavernous plexus, the latter from the interior of the corpora cavernosa, and penetrate through openings in the cortical network. This relation is of great importance in erection, since, as a necessary consequence of filling the cortical network, which, as already stated, is the principal reservoir, compression of the returning veins must ensue. In the crura penis the venous channels belong to the system of the venæ profundæ. As Langer has shown, these are not direct continuations of the great erectile veins, but are derived from the fine branchlets given off from them.

According to Langer's authority, therefore, the erectile tissue of the corpora cavernosa penis is to be regarded "as a broadly-expanded rete mirabile, which, in relation to the dorsalis, is unipolar, but to the venæ profundæ bipolar." We must agree with Langer, too, that there is an outer and inner portion to be distinguished. The outer consists of anastomosing veins lying close together—rete mirabile venosum (Kohlrausch, Jarjavay). This portion represents the proper erectile tissue of the urethra. The inner portion is a venous network of the urethra itself, and consists of small longitudinal and almost parallel vessels, which are connected with one another by numerous short and tortuous anastomoses. The outer portion is directly continued into the bulb as an erectile plexus; the inner subserves the character of a venous network throughout the membranous and prostatic portions and extends to the bladder.

The arteries furnish some twigs which reach the mucous membrane of the urethra, and there become capillary, and others that supply the corpus cavernosum ending likewise in capillaries.

The circulation of the corpus cavernosum always terminates abruptly by capillaries. The trunks of the returning venous blood—venæ efferentes—develop themselves from smaller vessels.

The vascular system of the glans is similar. Here, too, the spongy tissue is a rete mirabile venosum derived from capillaries (Hausmann, Kobelt, Jarjavay). The coarse network of veins, as we have already stated, is crossed by a close and fine network; from the most superficial capillary nets numerous loops extend up into the papillæ of the glans, and finer veins returning therefrom open into the peripheral cavernous spaces of the same structure. The branches of these loops are distinguished by their tortuous course (Langer); indeed, many of them are quite like tendrils.

The communication of the erectile body of the glans, with that of the urethra is effected by the efferent veins of the glans and the relation is such that the finer twigs of this venous plexus lie in the glans, while the coarser lie in the corpus cavernosum urethræ.

This plexus of veins lies on the dorsal side of the penis and was first recognized by Kobelt. It also reaches out between the corpora cavernosa penis and corpus spongiosum urethræ, and appears to constitute an especial cavernous body, for smooth muscular fibres occur in the trabeculæ and it is frequently enveloped by a feeble tunica albuginea.

Fig. 239.

Fig. 239. Transverse section through the injected gland. *a*, epithelium of the urethra; *b*, tunica mucosa; *c*, corpus cavernosum urethræ; *d*, corpus cavernosum glandis; *e*, mucous membrane of the glans; *f*, epithelium of the glans. System No. 2. Ocular No. 3. Hartnack.

The mucous membrane of the glans is clothed with a laminated pavement epithelium from 0.12 to 0.14 millim. in thickness, and is distinguished from that of the urethra by being less transparent and, further, by the fact that the uppermost cells are more strongly flattened, and are fused with one another. The nuclei of these cells are all rod-shaped. In the middle layers there are well-formed ribbed cells, while the lowest layer is composed of cylindrical epithelium, the cells being crowded together, so as to display somewhat the appearance of a stockade. The mucous membrane is rich in elastic-fibre networks, and has single or branched conical papillæ closely grouped together. They are more highly developed in Adults than in new-born Children.

Nerves are very numerous in the glans, and, according to Kölliker, end in Krause's club-shaped extremities found in the papillæ.

In the prepuce we generally find the same structure as in the skin. The epithelium of the inner layer, however, approximates in appearance the laminated pavement variety.

In the skin of the penis, as well as in the outer and inner lamina of the prepuce, there are sebaceous glands. In the latter place they measure 0.6 millim. in the long diameter, and 0.35 millim. in the transverse. These glands (glandulæ Tysonianæ) reach as far as the corona glandis, at the same time that the size and number of their diverticula gradually diminish. In new-born Children they are abundantly and well developed on both sides of the prepuce. In Adults it is sometimes hard to find them. In general, sebaceous glands are not found in the glans penis; still Schweigger-Seidel, in one instance, has seen the simple forms at the apex of the glans. Structurally these glands of the foreskin are quite similar to sebaceous glands elsewhere.

The urethra of all Mammals passes through the penis; of Birds only the Ostrich, some gallinaceous, and a few web-footed Birds have a true penis.

In the Turtle, among Amphibians, the sexual organ is single; in Snakes and Lizards it is double. The penis of Birds and Amphibians is not pervious, but simply has a channel for escaping semen (Leydig). Corpora cavernosa are pretty general in the penis of Mammals; in Birds cavernous tissue is about the penis or in the interior (Struthio).

Most Amphibians, too, have erectile tissue, and this either surrounds the penis in the form of a sheath (Saurians) or is well developed in the penis and glans (Turtles and Crocodiles). In many Mammals bony plates occur in the penis. The Cat, for example, has a short bony plate at the apex of the glans above the urethra; this bony substance posteriorly towards the corona has a small roundish cartilaginous kernel. Around the bony lamina and cartilaginous mass the corpus cavernosum glandis is spread out in the form of a semicircle.

In place of the corpora cavernosa penis Cats have an adipose pad surrounded by a tough albugineous tunic and subdivided in sections by connective-tissue cords. A feeble lamina of large veins stretches up by the side of the pad from below. These vessels form an intricate anastomosis with one another.

Female Sexual Organs.—Labia Pudendi.

We encounter in the labia majora all the elements of the skin.

The basis structure is a connective-tissue framework which, springing from the deepest portion, radiates out towards the periphery. Internally the texture is loose, forming the subcutaneous tissue; towards the epidermis it becomes tougher and thicker and constitutes the cutis. Where the texture is quite loose there are groups of fat-cells, large vascular and numerous nerve trunks; sweat glands and hair follicles, too, are represented in large numbers. The sebaceous glands are remarkable for their size—reaching a diameter of 0.5 millim.—and it is also curious that some open directly

on the free surface. Adjacent to the surface tolerably dense networks of elastic fibres are spread out flatwise; smooth muscular fibres are regularly interspersed between them (Henle). In regard to papillæ, nerves, Pacinian bodies and vessels, the labia majora do not differ from the skin of other parts.

Near the point of reflexion upon the labia minora the epidermis becomes more transparent; the uppermost cells are still firmly fused together, but the club-shaped nuclei within them are readily seen. On the labia minora we encounter well-marked laminæ of pavement epithelium, and the deepest cells in many instances, even in new-born Children, contain pigment granules about a rounded nucleus.

The mucous membrane contiguous to the epithelium has upon its surface close rows of vascular papillæ, in the form of cones with dilated apices.

The mucous tissue has no fat, and smooth muscular fibres are found in the connective-tissue cords. The framework of the mucous membrane shows the same character here as in the labia majora, for networks of stout trabeculæ are seen stretching from below up towards the periphery. Sebaceous glands without hairs occur in the labia minora except on the inner side; they measure 0.2 millim. in diameter, and are therefore smaller than in the labia majora. They are not found at the time of birth.

The twigs, which are given off from the branches of the labialis posterior, enter the papillæ as simple loops running tortuously.

The capillaries form networks on the surface and in the substance of the labia minora; from these, plexuses of fine veins are derived; these latter appear everywhere crossed by the capillary network (Gussenbauer). Accordingly, the labia minora, like the glans clitoridis, have an erectile tissue (Gussenbauer).

Clitoris and Vestibule.

The mucous membrane, as præputium and frænulum, is in direct communication with the labia minora and mucous membrane of the vestibule. Structurally, that is, in point of epithelium, mucous tissue, papillæ, and nerves, it is very similar to the labia minora.

The mucous membrane of the clitoris envelops the corpora cavernosa and glans, and this latter is in connection with both bulbi vestibuli. The latter correspond to the cleft corpus spongiosum urethræ in the Male. The corpora cavernosa of the clitoris, as well as the bulbs of the vestibule, are also enclosed by a fibrous tunic, and, as in the Male, have large venous plexuses, in the interspaces of which are found numerous smooth muscular fibres. In other respects they are similar to the corresponding parts of the Male, and here, too, have a direct connection with the vascular loops of the papillæ.

Gussenbauer, in an exhaustive description of the vascular distribution in the external sexual organs of the Female, has confirmed the long-asserted analogy between the corpora cavernosa penis and clitoris by proving the following points:—

First, that towards the root of the clitoris the small arteries discharge their blood directly into larger veins.

Second, that towards the surface arterial blood is received into the finer venous plexuses through minute arterial twigs.

Finally, that the capillary network under the surface, into which the arteries empty, especially towards the anterior end, is, together with the finer venous plexus connected with it, the medium for communication with the coarser erectile tissue.

The erectile labyrinth of the bulbus vestibuli is analogous in structure to that of the clitoris. The outer surface of the bulb has a coarse venous network, the inner a finer one. Through the interstices of the latter, veins press in, to join, within the submucous tissue of the urethra and vestibulum, the venous network that is spread over the anterior wall of the vagina, as far as the bladder (Gussenbauer).

In the process of erection the venæ profundæ hold the same important relation to the cortical layer of the erectile body, as in the penis. The relation, too, between other veins and the bulbo- and ischio-cavernous muscles is notable; for when these latter contract they compress the returning veins in the cavernous bodies of the clitoris and bulbus vestibuli. The pars intermedia—a venous plexus derived from the posterior surface of the clitoris—is the medium of communication between the corpus cavernosum of the clitoris, the bulb, nymphæ, frænulum and glans.

The mucous membrane of the vestibule is marked by numerous folds: numerous mucous follicles open on the free surface; they are irregularly distributed over the vestibule, and never occur in closely crowded groups except at the orifices of the urethra and vagina. They are, essentially, branched tubes, provided at the deeper portions with a number of dilatations, and in every instance are clothed with a single epithelial covering; the laminated pavement epithelium of the mucous surface is only found at the orifice of the duct. The size of the glands varies between 0.5 and 2.5 millim. The glands of Bartholine, which discharge at the side of the vaginal entrance, are quite similar in structure to Cowper's glands of the Male. They are ovate in form, and lie along the posterior border of the uro-genital diaphragm. They also hold an important relation to the muscles of the perinæum, for they are more or less enveloped by them, and indeed some solitary muscular bundles pass in between the glandular lobules. This is especially true of the bulbo-cavernous (accelerator urinæ) muscle. The excretory duct is from 15 to 20 millim. long, its wall is 0.2 millim. thick, its lumen measuring from 4 to 5 millimetres (Henle).

The duct is invested throughout with cylindrical epithelium excepting at the orifice, where there are laminæ of pavement cells. After dividing and subdividing it terminates in numerous half-spherical or ovoid diverticles—acini. These acini are furnished with cylindrical epithelium of various lengths and correspond in every respect with those in Cowper's glands.

Lying near the mucous surface are networks of vessels with which the vascular loops of the papillæ are connected; nerves having medullated fibres (sympathetic and pudendal), are also frequently met with, especially in the mucous membrane of the glans. Krause's club-shaped termini and the Pacinian bodies have been observed in these nerves.

Hymen and Vagina.

At the entrance of the vagina the mucous membrane forms a duplicature—the hymen. The epithelium is laminated and has about the same thickness as in the vestibule, viz.: from 0.3 to 0.5 millim. The delicate mucous membrane, rich in blood-vessels and nerves, with its single and multiple, long and conical, branched and unbranched papillæ, projects into the epithelial coat. The papillæ are closely crowded together and measure from 0.2 to 0.3 millim. in length.

The mucous membrane of the vagina is uneven, and especially in the vicinity of the vaginal entrance, both on its posterior and anterior wall, is distinguished by transverse fold-like or broad papillary elevations which are

richly supplied with capillary networks. The surface of each fold is marked at intervals by furrows of varying depth, which divide it into groups of large, broad and solitary papillæ.

The vaginal mucous membrane is lined with pavement epithelium, some 0.6 millim. in thickness, and has a framework of connective tissue with which numerous elastic fibres are associated, and from which tissue the papillæ, supplied with vascular loops, stretch upwards into the epithelium.

The submucous tissue is loose in texture, and, as we shall show presently, contains numerous vascular nets. The muscular tunic, adjoining the mucous coat and connected with it, is arranged in two layers, an inner or longitudinal, the stouter, and an outer or circular. Both these tunics are connected by oblique intersecting bundles.

From the internal layer muscular bundles also enter the submucous tissue and pass through into the tunica mucosa, terminating in the papillæ. The bundles of the muscular coat are separated by a pretty large amount of connective tissue, so that it does not appear homogeneous throughout; externally is a layer of loose connective tissue, upon which the external venous plexus lies. All the coats diminish in thickness as they approach the fornix. The finer vascular subdivision in the mucous membrane of the vagina is as follows:—

The arteria vaginalis enters the vagina from behind and gives off branches for the anterior and lateral walls before reaching the muscular coat. These arterial branches, after obliquely penetrating the muscular tunic, either break up into a submucous capillary network or furnish small twigs to the papillæ. In the upper portion of the vagina one vascular loop enters the papillæ, but in the lower portion several. The capillary loops of the compound papillæ, after anastomosing freely, unite to form a meshwork from which the central venous vessel of the papilla is supplied with blood. In the folds there are numerous veins of large size, plexiform in distribution, together with smooth muscular fibres, derived from the muscular tunic, as before described. This venous plexus can be regarded, therefore, as a cavernous structure (Gussenbauer). The veins entering the submucous tunic form meshes corresponding to the long axis of the vagina. These veins unite to form stouter trunks which pierce through the muscular coat and constitute the plexus vaginalis. In the walls of the plexus there is the same system of trabeculæ as in other erectile organs.

The vaginal mucous membrane is richly supplied with lymphatics and nerves; little is known in regard to their finer subdivisions. In those trunks which are made up of medullated fibres ganglion cells occur singly or in groups; the latter are chiefly found in those places where two or more trunks unite. The ganglion cells are also of two sizes, as was observed in the Male sexual organs.

URETHRA.

The epithelium covering the mucous membrane of the upper portion of the urethra consists of the transitional variety in, laminæ. The uppermost cells are club-shaped, truncated cylinders; lower down they gradually diminish in longitudinal diameter, until rounded and pavement cells compose the layer upon the basement membrane. In the outer portions we find laminated pavement cells as in the vestibule and vagina. The epithelium gains in thickness, too, as it nears the orifice. The mucous coat presents two divisions with a somewhat uncertain line of separation between them; an inner, the tunica mucosa, from which numerous papillæ press into

the epithelium, and an outer, the tunica submucosa; in the latter lies the cavernous tissue, formed of a stout venous network.

The thickness of the tunica mucosa amounts to about 0.13 millim.; that of the submucous tissue is more than five times as thick.

The tissue of the tunica mucosa is interspersed in many places with cells similar to lymph corpuscles; often, indeed, this infiltration is so extreme that the mucous tissue consists only of a delicate network, which is completely filled with cellular bodies (agglomerations of gland substance, Henle). In such places no distinct line of separation can be observed between the cells of the tunic and those of the deeper epithelial layer.

Littre's glands occur in the mucous membrane of the Female urethra as in the Male. They are more numerous near the urethral orifice than elsewhere.

The muscular sheath consists, chiefly, of an inner and outer layer; the former being longitudinal and continuous, having a breadth of 1.8 millim., whereas the latter is made up of circular fibres; this circular coat also is somewhat stouter than the longitudinal, and while, within, the fibres are smooth, without they belong to the transversely striated urethral muscles. The bundles in this layer are less closely grouped together than those in the longitudinal.

Finally, in some places there is added another longitudinal layer 0.2 millim. in thickness, in which only smooth muscular fibres are met with. Outwardly, the muscular tunic is enclosed by a fascia, almost 0.2 millim. thick, and which consists of wavy connective-tissue bundles running a parallel and usually circular course. The inner longitudinal muscular tunic is not wholly separated from the submucous tissue, for, on the one hand, it enters the latter in the form of small bundles of smooth tissue, having a longitudinal direction, and, on the other hand, the venous plexus of the submucous tissue is partially placed in the muscular tissue.

The venous networks of the submucous tissue, as well as of the vaginal plexus, are to be regarded as cavernous structures.

In Mammals the vagina is non-glandular as in the Human Female.

Both the clitoris and penis of many Mammals have bony plates and Pacinian bodies.

No one has yet observed external sexual organs in the Female of Fishes, Amphibians, or Reptiles.

In the Triton and in some larvæ of the Batrachians the mucous membrane of the cloaca has ciliated epithelium. (Salamandra maculata, rana) (Leydig).

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CHAPTER XXX.

THE UTERUS, PLACENTA, AND FALLOPIAN TUBES.

BY DR. R. CHROBAK.

I.—THE UTERUS.

[The microscopical investigations described in this chapter were completed at the Physiological Institute of Vienna.]

THE peritoneal fold investing the uterus is an exceedingly delicate membrane; on the anterior surface of this organ it extends downwards as far as just below the constriction, corresponding to the orificium internum, and on the posterior surface it reaches to the insertion of the vaginal wall in the cervical portion;* from these points it passes off anteriorly and posteriorly to form, respectively, the vesico-uterine and recto-uterine excavations. Anteriorly, the membrane is more firmly adherent to the muscular tissue than posteriorly, and so marked is this, that one portion cannot be dissected up at all, or only with great difficulty. This inseparable part represents a triangle whose apex is situated at about the middle of the anterior surface of the uterine body, and whose included angle points downwards.†

At the lateral margins an intimate apposition of the peritoneal folds exists, but only to a point about one centimetre below the oviduct; here the laminæ diverge from one another to permit the passage of the blood-vessels, lymphatics, and nerves into the uterine substance.

The great mass of the uterus consists of smooth muscular fibrillæ which show a varied lamination; at the present time, however, considerable irregularity prevails in classifying them, since the isolation of all the separate layers is impossible even in the pregnant organ.

If we follow the development of these muscular tissues, the simplest plan is to assume three layers: an inner one, consisting mostly of circular fibres; a middle, containing longitudinal fibres principally; and an outer or accessory.

The external muscular, though by far the weakest, is the most independent coat, and lies immediately under the peritonæum, to which it is attached; it is prolonged over the appendages of the uterus, and contributes more largely to them than the other coats do. Its composition is chiefly due to a bundle of longitudinal fibres, which take their origin on the posterior uterine wall at the cervical boundary; it is also strengthened by such accessory fibres as come to it from the sides; these overlay the fundus, and, diverging there, pass on for the most part to the ligamenta rotunda.‡

Under the head of the second layer, and separated from the preceding by several transverse bundles, are some strong muscular bands that pass over the fundus from behind forwards; they then bend backwards and forwards,

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* Luschka, *Anatomie*, 2 Bd. 2. Abth. S. 360.
† Henle, *Anatomie*, 2. Bd. 2. Lief. S. 486.
‡ Hélie, *Recherches sur la disposition des fibr. muscul. de l'ut.* Paris, 1869.

intersecting various other short fibres.* This layer is said to be united with the preceding at one point only, viz., the middle of the base of the uterus.†

The last layer that is demonstrable, like the first, does not involve the lateral walls of the uterus; it includes numerous bundles of fibres, mostly transverse, smooth, and short, crossing one another in the most different directions, and sending occasional prolongations to the ligaments. The general fact alone is clear, that the fibres which anteriorly were superficial become lost posteriorly in the interior, and *vice versâ*.

This coat, which far exceeds the others in strength, is recognized by the remarkable size and thickness of the walls of its vessels. This is especially marked in the pregnant organ.

The innermost coat, Luschka says,‡ can be regarded as the fundamental one, because there can be shown in it traces of its being, at one time, made up of two lateral halves; it consists principally of circular fibres, which, originating in layers of circular fibres from the uterine part of the Fallopian tubes, develop into gradually increasing rings which meet in the median line, and these fibres not only form the basis structure of the corpus uteri, but they can also be traced in the cervical portion, and even detected in the vaginal wall. (To this circular fibre-coat belong the so-called sphincters which are found at the orificia externum and internum.) Besides this well-pronounced circular fibre-layer, there is a three-sided muscular lamina: in the anterior and posterior wall of the uterus it consists of a band of longitudinal fibres pointing downwards; from it fine bundles of muscular tissue can be traced into the mucous membrane.§ In the portio cervicalis regular fibrillation still further disappears,‖ and there appears again a tendency to grouping in three separate layers (Henle); the arrangement is such that the circular fibres of the innermost uterine lamina form the middle, which is certainly the strongest coat; this is invested externally by longitudinal fibres that are for the most part lost in the neighborhood of the bladder, the vagina, and the urethra; the internal lamina consists, too, of longitudinal muscles, which supply the mucous membrane with fibres, and intercalate with the fibres of the sphincters of the os uteri externum and internum. (The sphincter of the orificium internum forms an isthmus three millim. long (Guyon).¶) Contractile fibre-cells are the chief components of all these uterine coats, and a firm cementing substance binds them so intimately together in bundles and laminated muscular bands that isolation is very difficult. Lastly, the bundles are themselves held together by an abundance of nucleated connective tissue and occasional elastic fibres.

The fibre-cell of the normal uterus is fusiform, and often has very long ends; during pregnancy, however, the contractile elements attain such a development (no reference is made to new formations) that their length increases from 0.045 millim., their normal measurement, to 0.660 millim., and their breadth, which before amounted to from 0.009 to 0.014 millim., now may increase to 0.074; here we repeatedly meet with muscular fibres whose margins are bevelled down and indented. These cells, when seen in transverse sections, have a roundish, ovoid contour, with from three to five angles, and, consequently, when considered as a whole, have several edges.

The substance of the cell will be found clear and transparent only if the

* Pappenheim, *vorl. Mittheilung.* Korn and Wunderlich, *Vierteljahrschrift*, 3. J. 1. Heft.

† Hélie, loc. cit. ‡ Luschka, loc. cit. § Hélie, loc. cit.

‖ Retzius, *Struktur des Uterus;* Froriep's *Tagesberichte* in Canst. *Jahresbericht*, 1850, Bd. 1. S. 64.

¶ Guyon, *Etude sur la cavité de l'utérus à l'état de vacuité. Journ. d. Physiol.* II.

part examined be fresh and belong to the first two-thirds of pregnancy; it then exhibits very uniformly a nucleus containing granules at both ends (Arnold).*

The nucleus, always single, is elliptical, fusiform, or club-shaped; it varies in length from 0.002 to 0.015 millim., and in breadth from 0.001 to 0.003 millim. (Frankenhäuser),† (these proportions, however, increase twofold during pregnancy), and lies most frequently in the enlargement corresponding to the middle of the cell; often enough, however, its position is asymmetric (in the parietes). A controversy still exists regarding the structure of the nucleus and its bright granules (Hessling,‡ Frankenhäuser, § Arnold.‖)

The measurements just given are not true of the muscular fibres in all the coats, but only in those that have an important function to perform during parturition. Accordingly the most superficial fibre-cells are shorter, more slender, and more cylindrical; the same is true, too, of the muscle-cells in the internal lamina, for their length amounts to from 0.018 to 0.034 millim. only (Kölliker¶). None of these exhibit any considerable growth during pregnancy.

The mucous membrane of the uterine body terminates in a well-defined border at the upper end of the isthmus of the cervix;** in the virgin state it is from 1 to 1.8 millim. in thickness, gray or pink, and becomes gradually thinner as it approaches the cervix and orifices of the oviducts;†† no well-defined line of demarcation separates it from the underlying or muscular coat, and in fact it can only be isolated in small fragments. The surface is smooth excepting only about the orifices of the tubes, where it presents very slight foldings but no papillæ (Hennig‡‡).

Again, it is covered, in health, with a thin layer of a more or less gray, translucent, and somewhat glutinous fluid of slightly alkaline reaction; this contains in various and slight proportions cylindrical cells, little roundish granular cells—secretions from the uterine glands, occasional cilia, and very seldom intact ciliated cells (in old people we find, too, cholesterine, monads, algæ, free fat, etc., Donné, Taylor, Smith, Scanzoni and Kölliker, Hennig, Schlossberger, Hausmann, et al.).

The mucous membrane of the uterus has no frame-work of connective tissue. Henle§§ claims that he has occasionally succeeded in demonstrating a fine network of pale fibres by pencilling with the brush. This was accomplished by first treating the tissue with caustic potash.

This framework really consists, however, of the uterine tubular glands, immediately to be described, between which there seems to be a mass of free nuclei from 0.006 to 0.008 millim. in diameter, together with much elongated cells or various sorts of polyhedral or little plate-like cells, fibre-cells in the most various stages of development, a proportionately large amount of interstitial substance, and bundles of muscular tissue reaching from the innermost layer of the muscular coat to the base of the glands.

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* Arnold, see page 145 of this Handbook.

† Frankenhäuser, *die Nerven der Gebärmutter.* Jena, 1867.

‡ Hessling, *Gewebelehre*, 1866.

§ Frankenhaüser, loc. cit.

‖ Arnold, loc. cit.

¶ Kölliker, *Zeitschrift f. wissensch. Zoologie.* Bd. I.

** Virchow, Fror. und Schleiden's *Notizen, über die Bildung der Decidua.*

†† Robin, *Mémoire pour servir à l'histoire anat. de la membre muqueuse de l'ut. Arch. général.* Juillet, 1847.

‡‡ Hennig, *der Katarrh*, etc.

§§ Henle, loc. cit.

The glandulæ utriculares were first mentioned by Malpighi,* then successively by Baer,† Burkhardt,‡ Eschricht, and E. H. Weber,§ later by Krause,‖ Sharpey,¶ Reichert,** and Bischoff,†† and were finally a second time described by E. H. Weber,‡‡ and since by others.

They present, in the Human species, a uniform type, though two forms are apparent in many animals; some individual cases are still giving occasion for controversy, as the Bitch, for instance; compare Sharpey, §§ Ercolani, ‖‖ and Friedländer. ¶¶

They represent, usually, single tubes of varying length; often, however, they have one or more diverticula at or below the middle; the general shape is cylindrical or somewhat club-shaped at the extremity, which terminates blindly; they discharge into the cavity of the uterus at the surface of the mucous membrane. Here they are apt to be compressed laterally or upon three sides, and the diameter of the orifice is greater than of the calibre in other parts (Hennig ***).

They adopt most circuitous courses, and even wind spirally, like a corkscrew; thus the length of the follicles sometimes considerably exceeds the thickness of the mucous tissue.

On the whole, the inclination of the tubes is vertical to the plane of the membrane, and this is especially marked at the lower part of the uterine cavity and in the neighborhood of the tube-orifices; on the other hand, the ducts in the upper part of the body and at the base have frequently an oblique or nearly horizontal direction.

The base of these glands is very difficult to isolate in the normal uterus; in the menstruating or pregnant condition it is less so; it is also very seldom possible to obtain a complete view of it on cross section, because of its many turnings. It consists of an uncommonly thin, structureless membrane, in which we generally find ovate nuclei, especially in the menstruating organ. These bodies must be distinguished from the muscular nuclei which remain adherent to the follicular wall during the process of isolation.

The subject of the epithelium of the glands is so important that I insert here the description which Gustav Lott has given.

As early as 1852, Leydig ††† mentioned the fact that Dr. Nylander had observed ciliated epithelium in the uterine glands of the Sow.

Though Leydig, at the close of his article, expressed the supposition that a similar condition might reasonably exist in other Mammals and in the Human species, yet since that time no further observations on this point have been published.

Kölliker ‡‡‡ simply confirms Nylander's discovery. In Leydig's §§§ own manual of Histology, that appeared five years after the first report, he reaffirms his previous

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* Malpighi, Opp. 1687. Vol. II. S. 220.

† *Unters. über die Gefässverb. zwischen der Mutter und der Frucht.* Leipzig, 1828.

‡ *Observat. anatom.* Kas. 1854.

§ E. H. Weber, *Braunschweiger Naturforscherversammlung.*

‖ Krause, *Anatomie*, 2. Aufl. 1. Bd.

¶ Sharpey, s. Canstatt. *Jahres.* 1843, 1. Bd. S. 106.

** Reichert, Müller's *Archiv*, 1843.

†† Bischoff, *Entwickelungsgeschicht. d. Hundeeies*, and Müller's *Archiv*, 1846.

‡‡ E. H. Weber, *Zusätze zum Baue und der Verrichtung der Geschlechtsorgane*, 1846.

§§ Loc. cit.

‖‖ Ercolani, *Giamb. delle glandule otricolare*, etc., 1868.

¶¶ Friedländer, *Unters. über den Uterus*, 1870.

*** Hennig, *Catarrh der weibl. Geschlechtsorgane*, 1870.

††† Loc. cit.

‡‡‡ Kölliker, *Handbuch der microskopischen Anatomie*, 1852, Bd. II. pp. 445–46.

§§§ Leydig, *Lehrbuch der Histologie*, 1857, p. 518.

statement in regard to the Sow. Frey * does the same thing up to the latest date, and adds, that in the literature to which he had access, hardly any mention was made of the discovery. Becker,† who searched so carefully for ciliated epithelium in the genital apparatus of the Human female and several animals, does not allude to the uterine glands, and Hennig,‡ in describing the glands of the tube as seen by him, felt himself compelled to declare that the chief difference between the Human follicular organs and the simple mucous folds of the Fallopian tubes rested upon the deciduous ciliated facings of the mucous surface.

Henle,§ too, expressly says, that the only difference between the cylindrical epithelium of the glands and the epithelium upon the free mucous surface of the uterus, is that the former has no cilia.

The statements of others, too, about the epithelium we are now describing, differ materially from one another. It is true the majority of authors ascribe cylindrical epithelium to the Human female and most Mammals, yet all do not coincide in this.

Thus, in the first place, there are differences of opinion about the former, for while Weber,‖ Leydig,¶ Henle,** Kölliker,†† Frey,‡‡ and Hennig §§ speak of cylindrical epithelium, others, as, for example, Gerlach, ‖‖ Scanzoni,¶¶ Schröder,*** describe a pavement epithelium. Kölliker talks about the ordinary variety of epithelium, while Hennig and Henle expressly mention a non-ciliated. Leydig makes the following statement: "Probably there is no less vibration in the epithelium of the glands than over the rest of the uterine mucous surface." The views also held by many in regard to a similar condition in different animals do not entirely agree.

Leydig††† asserts that the glands of most Mammals have a ciliated cylindrical epithelium; Reichert ‡‡‡ and Ercolani §§§ state that the Rabbit has pavement epithelium, and this, Ercolani says, is true also of the Bitch and Mouse.

In regard to the Ruminants, Whole-hoofed Animals and the Sow, most authors agree that the little glands bear cylindrical epithelium; very lately, however, Friedländer ‖‖‖ published a work in which he described a vibrating cylindrical epithelium in the uterine (p. 25) and cervical (p. 457) glands of the Human female and in the uterine glands of the Bitch (p. 55). Friedländer puts the fact down without shedding any further light upon it, though he certainly did not find it well authenticated in the literature of this subject. This statement is the more remarkable since we have been able to convince ourselves that the task of bringing the cilia of questionable cells into view, when we use preserved specimens, is exceedingly difficult; this will be shown in what follows, and Friedländer does not explain to us the conditions under which he succeeded in getting a distinct view of the ciliary motion. If he used preserved specimens, as it would appear, we should very much like to become

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* H. F. Frey, *Handbuch der Histologie u. Histochemie des Menschen.* 3. Aufl. 1870, page 539.

† *Ueber Flimmerepithelium u. Flimmerbewegung im Geschlechtsapparate der Säugethiere und des Menschen.* Moleschott.

Untersuchungen zur Naturlehre des Menschen u. der Thiere, B. II. p. 71.

‡ C. Hennig, *Der Catarrh der inneren weiblichen Geschlechtsorgane*, 2. Aufl. 1870, p. 137.

§ J. Henle, *Handbuch der systemat. Anatomie des Menschen*, Bd. II. p. 460.

‖ E. H. Weber, *Zusätze vom Bau und den Verrichtungen der Geschlechtsorgane.* 1846. p. 33.

¶ *Lehrbuch der Histologie*, p. 487.

** J. Henle, *Handbuch der systematischen Anatomie des Menschen*, B. II. p. 460.

†† Loc. cit.

‡‡ Loc. cit.

§§ Loc. cit.

‖‖ J. Gerlach, *Handbuch der allgemeinen und speciellen Gewebelehre des Menschen*, 1850, p. 352.

¶¶ F. Scanzoni, *Lehrbuch der Geburtshilfe*, 4. Aufl. B. I. p. 50.

*** C. Schröder, *Lehrbuch der Geburtshilfe*, 1870, p. 22.

††† Loc. cit. p. 518.

‡‡‡ *Ueber die Bildung der hinfälligen Häute der Gebärmutter und deren Verhältniss zur Placenta uterina.* Müller's *Archiv f. Anat. u. Phys.* 1848, p. 78.

§§§ G. B. Ercolani, *Delle glandole otricolari dell' utero e dell' organo glandolare di nuova formazione, che nella gravidanza si sviluppa nell' utero delle femmine dei mammiferi e nella specie umana.* Bologna, 1868.

‖‖‖ Friedländer, *Physiologisch-anatomische Untersuchungen über den Uterus.* Von Dr. Carl Friedländer. Leipsic, 1870.

acquainted with his method. Friedländer's assertion, too, that he saw vibrating epithelium in the cervix of immatured Girls does not accord with the observations of numerous others.

Lott says that when the uterus of the Cow, Sheep, Sow, Rabbit, Mouse, and one species of Bat was examined in the fresh state, he saw a vibrating motion of the cilia throughout the entire length of the uterine glands. His examination of fresh objects resulted negatively in four cases; the uteri in question were respectively those of a Calf, a very young Guinea-pig, a gelded Sow, and a Mare that died of some pyæmic process.

In some cases he saw the glandular epithelium actively vibrating, while the mucous surface not only was entirely at rest, but also exhibited no cilia at all.

To obtain a good view of vibrating cilia, the best method has proved to be the following: first carefully snip off a piece of the mucous membrane you desire, then tease this little fragment apart with great care, and mount in iodized serum, aqueous humor, or a weak solution of common salt (1 per cent.)

The ciliary impulse was in most cases extremely active, though varying in continuance; for while in the Mouse and Bat, after the lapse of a few minutes, the motion ceased under the glass cover used in these examinations, the case was different in the Sheep, for under similar conditions the ciliary movement lasted for an hour or more.

Looking at the gland in longitudinal section, the direction of the ciliary impulse was uniformly from the base towards the orifice; while when seen in transverse section we observe a sort of turbinated motion from below upwards upon a spiral line.

It is not very difficult for the eye to follow one and the same tube, and obtain a view of it in different planes. This is especially true in the Cow's uterus, from the many and frequently sharp turns that each tube makes in its course, and all that is necessary is an appropriate movement of the adjusting screw.

Single cells, whose cilia were not in motion, though in good condition, Lott preserved by proceeding as follows: taking the Sheep's uterus, he removed a portion of the horn, and while still fresh, or after it had lain in iodized serum, he spread it out in such a way that by using the belly of a scalpel he could scrape the mucous membrane without cutting it. By this method of pressing off, as it were, we can obtain the epithelial tubes of the glands free from all surrounding connective tissue, and may frequently see the cells quite unaltered in position. Frequently, small pieces of the tubes that have been broken off, may be seen on the object slide in transverse section, so that here, again, we get a view of all sorts of planes of section.

We must prepare these objects either with iodized serum or with bichromate of potash (a cold saturated solution); this procedure renders the cells very transparent, and the nuclei and contours become sharply defined. In such preparations, even those mounted in iodized serum, he was now unable to see the cilia vibrating; they had already undergone a change, and yet were so far distinct in outline, that he could designate them as extremely short and fine, and as standing crowded together.

He found it equally impossible to recognize distinct cilia in those portions of the uterus, whether they had been first placed in Müller's fluid or in a 4 per cent. solution of the bichromate of potash, and then afterwards in alcohol; or, if after remaining in alcohol, they had been put into a 2 per cent. solution of the bichromate, or a 0.001 per cent. solution of the chloride

of palladium. Nor was he able to get a better view of the cilia after macerating them in a cold saturated solution of the bichromate.

In all these preparations, all that he saw was little bud-like prominences, regularly disposed along the internal border of the epithelium; they were in close rows and gave a general appearance of striation.*

The form and arrangement of these epithelial cells can be studied with greater nicety in hardened preparations; the most satisfactory prove to be sections first hardened in Müller's fluid, and then colored with carmine. A very small space in such objects affords us, too, a general view of the follicles in all possible planes, some real, some apparent; consequently, it is immaterial whether we cut horizontally or vertically through the mucous coat.

The cells are shaped like a club with hexagonal contour; the broad end is directed outward, and the tapering end towards the lumen; the latter corresponds to the long axis of the tube.

When we examine a follicle in transverse section, each cell presents the outline of an equilateral triangle, whose apex is truncated and directed inwards. According to the breadth of the tube, and kind of animal, these cells unite in forming a ring, or series of encircling rings, corresponding with the varying calibre of the gland. In proportion as the lumen becomes smaller, and the cells that form the ring diminish in number, so the shape of each cell approaches in like ratio that of an equilateral triangle: this internal epithelial coat, too, becomes narrower, in proportion to the smallness of the angle which the sides of each cell make in converging towards the apex. This view is corroborated also by the plates of Henle † and Kölliker, ‡ especially those of the former, while Kölliker only represents a few very wide tubes, in which, of course, the triangular form is not very prominent. Hennig § gives us a different view of the same thing, by representing the cells as floating almost separately in the follicular cavity.

On the other hand, sections made parallel to the tubes present the cells in the form of parallelograms whose long diameter always preponderates. Lott lays stress on this fact, in opposition to several authors, who assert that the Bitch (Ercolani),‖ Rabbit (Reichert ¶ and Ercolani), and Mouse (Ercolani), and Human female also (Gerlach,** Scanzoni,†† Schröder ‡‡) have a pavement epithelium. Notwithstanding this, however, Lott found this condition pronounced in all cases, though not equally so in all animals.

The only modification the shape of the cell undergoes is where the follicles make sharp turns in their course; at these points the cells, even when seen in the long axis of the tube, are observed to direct their apex to one side; those upon the convex side naturally pointing their extremities inwards; those upon the concave sides turning them outwards.

By employing our minute adjuster and examining our object throughout its different planes, we are also able to get a clear outline of the cell contour on the external and internal surface of the epithelial tubes, and so at last

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* In S. Th. V. Soemmering's work, the 6th volume, which is devoted to the construction of the Human body, and was edited by Henle, contains the following statement in regard to the cilia (Ed. 1841, p. 246):

"After death they first appear like very minute prominences, and then entirely disappear."

See Friedrich for the significance of the striation. *Einiges über die Structur der Cylinder- und Flimmerepithelium. Arch. f. path. Anat. u. Phys.* Bd. XV. p. 535.

† Loc. cit. fig. 538 and 539.

‡ Kölliker, *Handbuch der Gewebelehre*, 5 Aufl. 1867.

§ Loc. cit. Taf. III. Fig. 10.

‖ Loc. cit.

¶ Loc. cit.

** Loc. cit.

†† Loc. cit.

‡‡ Loc. cit.

complete our ideal representation of the cell we are studying. The outer extremity (the base of the club) of each cell assists in forming a beautiful tessellated work, which seems composed of tolerably regular hexagons. The inner superficies of this epithelial layer appears also made up of hexagons, which when seen in the long diameter of the tube are long, and in its transverse diameter are narrow (the tapering end of the club). The mosaic work is best seen in sections prepared in Müller's fluid.

He found the nucleus very large in most cases, especially in the Bitch, always single, and invariably situated in the outer portion of the cell, as both Henle* and Kölliker† represent it; while Hennig‡ describes the same body as lying, frequently, in a club-like thickening of the inner end, which Lott never saw. It is true, however, that Lott occasionally found the nucleus so large that it projected somewhat into the inner portion of the cell. This body, when fresh, appears coarsely granular and much more strongly refractive than the finely granular and more opaque protoplasma.

The slender extremities of the club-shaped cells, which are directed inwards, support the cilia; whether these appendages belong to all cells equally or not, Lott is unable to state positively; as we have seen before, however, it is extremely probable that such is the case: first, because of the uniform shape of all the cells; and secondly, because of the little bud-like processes which he described, and which he regarded as the remains of cilia.

In addition to the animals mentioned above, such others as the Cat, Bitch, full-grown Guinea-pig, Mare, and Human female were examined by using hardened preparations, and the epithelia were shown to agree in the characteristics we have mentioned. The epithelium of the mucous membrane is subject to constant change; § moreover, it is quite probable that the cells form anew after every menstrual period.

[The observed fact that the relative proportions of the parts forming the mucous coat vary exceedingly, and according to the existing stage of development, tends to show that continuous and unusually rapid changes take place in the formation of epithelium.

Thus, the thickness of the mucous membrane, that usually varies between 1.0 and 1.8 millim., measures from 4 to 8 millim. at the menstrual epoch; the follicles, too, which normally are from 0.03 to 0.1 millim. apart from one another, now press so closely together that only very narrow mucous ridges remain between them; their length, usually 2 millim. at the most, now reaches 7 millim.; their diameter rises from 0.05 to 0.1 during menstruation, and after conception to 0.24 millim.; lastly, the epithelial cells which clothe the mucous membrane and follicles, and normally are from 0.015 to 0.04 millim. high, attain during menstruation and pregnancy more than double their former volume.]

A well-defined line is drawn between the mucous membrane of the neck and body; the former is much the tougher, firmer, and more transparent of the two, and varies in thickness between 0.215 and 3.00 millimetres. An investment of connective tissue extends over the orificium internum quite into the corpus; it lies between the mucous and muscular layers, and is especially well marked on the posterior wall (Rokitansky,‖ Klob¶). The anterior and posterior surfaces of the mucous coat lining the cervical

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* Loc. cit. † *Gewebelehre.*
‡ Loc. cit. p. 13. § Kölliker, loc. cit.
‖ Rokitanski, *Lehrbuch d. pathol. Anatomie*, 3. Bd.
¶ Klob, *Pathol. Anatomie der weibl. Sexualorgane*, 1864.

canal exhibit the branching folds, known as plicæ palmatæ; the former are placed somewhat to the right of the median line, while the latter are a little to the left.* The substance of these folds is a firm tissue, rich in connective-tissue nuclei; it contains, however, few muscular fibres, and only occasional elastic ones. Lodged in the substance of these ridges, excepting only in the lower and smoother part of the cervical canal, we discover the so-called "mucous follicles of the cervix."

These follicles present the following characters: they are usually round or flattened on the sides, or may be compressed together in folds if they are not full; their size varies very much, and always depends upon the thickness of the mucous membrane; they open upon the free surface by an orifice from 0.1 to 0.3 millim. in diameter, or by a short and broad excretory duct; the contents discharged consist of a strongly alkaline mucus capable of being drawn out in threads, and perfectly transparent, though coagulable in alcohol. Friedländer describes beaker-cells which he found in this mucus.

The references made by the same author to two kinds of glands seem to be practically as follows: The finest mucous follicles which belong to infancy are, in Adults, drawn out like tubes by the growth of the mucous membrane; their own growth during puberty obliges them to fill out in proportion to their length. They consist of a structureless membrane, which, however, is so firmly united to the connective tissue and the muscular fibres embracing the glands, that isolation is impossible.

These glands are lined with a cuboidal epithelium, and the nuclei, as usual, are placed nearer the wall than the lumen.

In the lower half of the cervix the mucous membrane exhibits slender, minute papillæ between the glandular orifices; they are 0.2 millim. high, covered with ciliated epithelium, and each possesses a vascular loop (Kölliker,† Hennig,‡ Taylor Smith,§ and others).

(Hjalmar Lindgren mentions also a thin layer, having no cells, and immediately under the epithelium; it is said to be traversed by out-runners from the connective-tissue corpuscles.)

The ciliated variety of cylindrical epithelium may prevail throughout the entire extent of the cervical mucous tissue, or only in the upper two-thirds; the parietal extremities of the cells frequently seem to gradually taper into fine threads (Friedländer). As we approach the os uteri externum, we observe stratified epithelium, showing all the transitional forms up to the pavement variety.

Besides these little glands just described, we find little closed sacs occurring regularly, and differing only in numbers and distribution. They are from 0.3 to 5 millim. in length, and consequently often extend into the muscular coat. These bodies, the ovula Nabothi, are clear or slightly yellow in appearance, and are to be regarded partly as new formations and partly as retention-cysts (Rokitanski, ‖ Förster,¶ Hirsch,** Kölliker, †† Virchow, ‡‡

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* Hjalmar Lindgren, *Studier ofver lifmodrens byggnad hos menniskan.* Canstatt. *Jahresb.* 1867, 1. Bd. S. 25.

† Kölliker, *Gewebelehre.*

‡ Hennig, *Catarrh d. weibl. Geschlechtsorgane.*

§ Taylor Smith, *Med. Chir. Transactions*, XXXV.

‖ Rokitanski, loc. cit.

¶ Förster, *Handbuch der allgemein. Pathol. Anat.*

** Hirsch, *Ueber Histologie und Formen der Uteruspolypen.* Dissert inaug. Giessen, Canst. *Jahrb.* 1855, 2. Bd.

†† Kölliker, loc. cit.

‡‡ Virchow, *Krankhafte Geschwülste*, 1. Bd. 264.

et al.). They are even found on the outer surface of the vaginal portion of the uterus.

During pregnancy and the time of the catamenial flow the mucous membrane in the cervix takes part in the general growth; the ridges diminish in the same ratio as the mucous follicles, now measuring from 1 to 2.75 millim., enlarge, so that nothing remains of the mucous coat but a delicate trabecular structure 3 millim. high; the mucous glands, on the other hand, have both a larger and more succulent epithelium, and secrete the abundant mucus which occludes the cervix during gestation.

At the outer surface of the vaginal portion every fold and granular formation disappears. The glands of the portio vaginalis, described by Robin * and Wagner,† have never been observed a second time, at least in a normal case; ‡ on the other hand, the mucous substance possesses a great number of simple or compound papillæ, each about 0.5 millim. high, provided with a vascular loop, and covered with a thick, indeed often tenfold, layer of epithelial cells.

The epithelium itself—very easily separable as a whole—possesses cylindrical cells in the lowest layer; as one ascends, however, they become gradually flattened down, and are club-shaped, elliptical, or spinous, until finally in topmost layers we find nothing but thin little plates, which are united together by a proportionately great quantity of cement-substance.

The nerves that originate from the cervical and neighboring ganglia and plexus hypogastricus enter the muscular coat by the ligamenta lata, along the border of the portio cervicalis; without always following the course of the vessels, they spread themselves out symmetrically on the anterior and posterior sides of the organ. Generally speaking, the neck is said to contain more nerves than the body; nervous filaments may be traced quite up to the mucous tissue (Kilian);§ on the other hand, the mucous membrane of the fundus is said to be more sensitive than any other part (Lazarewitsch ‖ et al.).

The uterus possesses medullated and non-medullated or pale filaments, and, according to the investigations of Frankenhäuser,¶ Koch,** Kehrer,†† Luschka,‡‡ Polle, §§ and others, the submucous ganglia, with which from two to three pale nerve-fibres communicate, show the same relation; at least this is the case with animals.

Further classification of the nerves is impossible at the present time, since their mode of termination in the mucous substance is unknown. It is true, Kilian, Polle, and others describe the passage of nerve-fibrils into the papillæ in the cervix; Hjalmar Lindgren even finds a delicate network of pale fibres between which were little masses, finely granular and strongly refractive; these fibres, resolving themselves into tufts, penetrate to the epithelium; the nervous character of these fibres, however, is not entirely free from doubt.

The distribution of the nerves in the muscular tissue of the uterus has received a good deal of study lately.

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* Robin, *Gazette des Hôpitaux*, 1852, 11.

† E. Wagner, *Arch. f. Physiol. Heilkunde*, XV. S. 495. ‡ Friedländer loc. cit.

§ Kilian, *Nerv. des Uterus. Zeitschr. f. ration. Medic.* 1851.

‖ Lazarewitsch, *The Lancet*, 1867, No. 17.

¶ Frankenhäuser, *Jenaische Zeitschrift*, 1864, 1. Hft.

** Koch, *Ueber das Vorkommen von Ganglienzellen an den Nerven des Uterus.* Göttingen, 1865.

†† Kehrer, *Beiträge zur Geburtskunde*. 1864. ‡‡ Luschka, loc. cit., S. 378.

§§ Polle, *Die Nervenverbreitung in den weibl. Genitalien.* Göttingen, 1865.

Frankenhäuser * says that the pale nervous fibrils which originate among the darkly-contoured ones form nets about the muscles, and finally, after being developed to filaments having nuclei or little nodules (Knötchen), terminate in the nucleus of the muscle cell (Arnold †).

We find also, during pregnancy, an undoubted increase of the nerves in size (W. Hunter, Tiedemann, Remak, and others); at this period, too, Kilian says, we may trace the medullated nerves further than in virginity.

The blood-vessels of the uterus originate from the arteria uterina hypogastrica, arteria uterina aortica (Luschka), and from the arteria spermatica externa; the veins unite to form two plexuses, the uterine and pampiniform.

The two first-mentioned arteries, arching over the uterus, meet on the lateral border, where pretty good-sized trunks penetrate the muscular substance, and then, branching rapidly, inosculate by capillaries with their fellows of the opposite side (Hyrtl ‡). They also envelop the muscular bundles and penetrate to the mucous membrane.

Arrived here, the glands are next invested with capillaries, and finally an irregular net of broader vessels is formed near the surface, from which delicate, valveless veins take their origin.

In the portio cervicalis the distribution of vessels is much more regular, but the thickness of their walls is so disproportioned that the calibre of each vessel is only about a third of its gross diameter (Henle). The vessels that pass vertically to the surface of the cervical canal, through the parietes of the mucous follicles, constitute a very superficial network which furnishes a vascular loop for every papilla.

Nearer the labia we observe delicate arteries that are a little tortuous or spiral in their upper portion; they also make a capillary net immediately under the epithelium, provide the papillæ with loops, and are the source of returning veins.

[The blood-vessels, which become enlarged to an enormous extent after conception, experience a growth and new formation of contractile elements.]

The lymphatic vessels form large networks and plexuses immediately under the peritonæum in the peripheral layers of the pregnant uterus. The branches derived from the fundus pass to the pampiniform plexus to connect with the lymphatic glands of the lumbar region; those from the cervix join the lymphatic glands of the small pelvis.

The absorbents of the interior of the uterus are practically unknown.

Hjalmar Lindgren says, the lymphatics of the neck form arches, from which blind outrunners with sinuous borders stretch towards the epithelium.

Method of Investigation.

For studying the coarse fibrillation of the uterus to the best advantage it is well to use the pregnant organ, either in the fresh state, or slightly hardened in alcohol, or in a mixture consisting of 1 part muriatic acid and 90 parts alcohol, kept heated a considerable time. To study the uterus in cross-section, the method of subjecting alcoholic preparations to drying in the air (Lufttrocknung), or boiled preparations to immersion in pyroligneous acid, is worthy of recommendation.

For isolating the muscular fibres we employ very dilute chromic acid (.1 to .01 per cent.), chromate of potash, iodized serum, caustic potash,

* *Nerven der Gebärmutter.* † Loc. cit.
‡ Hyrtl, *Topograph. Anatomie*, 1860, 2. Bd. 180.

acetic acid (1 to 2 per cent. strong), 20 per cent. solutions of nitric acid, Moleschott's fluid, $\frac{1}{2}$ per cent. solutions of nitric acid, heated to the boiling-point; for the most minute nerve branchlets we employ pyroligneous acid and glycerine combined.

For coloring use carmine, aniline, nitro-saliculic acid, chloride of palladium, and chloride of gold. The most important point of all, however, is to make use of the very freshest preparations, which should be kept moist in an albuminous solution or iodized serum.

II.—The Placenta.

[This article has been contributed by Dr. Reitz, of St. Petersburg, and the researches connected with it have been performed under my direction.—Stricker.]

It is well known that the placenta of the Human female is made up of two parts, a maternal and fœtal, both of which have the most intimate connection from the fourth month of pregnancy. The maternal part, or uterine placenta, which is from one-quarter to one-half a millimetre thick, consists principally of large cell-elements. In general the cells are finely granular and very variable in shape; they have large, roundish, distinct nuclei, which contain one or more nucleoli; sometimes several nuclei are present; many cells, too, are provided with longer or shorter processes. There are, also, between these cells occasional large vesicles with aggregated nuclei; Kölliker* has given a description of them.

Usually the cells lie so closely together that they constitute almost the entire thickness of the uterine placenta; the most frequent arrangement seems to be that of clusters, less often they are quite single. In all cases they are embedded in the basal substance that in some places has the appearance of fibrillated tissue, and in others looks like a hyaline mass containing fine granules. Between these cells I found† other immense cells, capsulated and having large vesicular nuclei and nucleoli; from being stored away in capsules, from their considerable size, their nuclei, nucleoli, and granular contents they bore a striking resemblance to ganglion-cells. Ecker‡ was the first to describe the smooth muscular fibres of the uterine placenta. Kamenew§ followed him. All other investigators emphatically denied their presence; in my examinations I have always succeeded in detecting these smooth muscular fibres in the outer layers of the placenta. They were present in considerable quantity, and often were arranged in laminæ; in isolated preparations, treated according to Jassinki's‖ direction with muriatic acid, a distinct, well-marked, staff-like nucleus could be demonstrated in many of the cells. A considerable number of spindle-shaped cells are also to be found in the different layers of the uterine placenta, but their character cannot be very accurately determined.

The tufts of the uterine placenta, which serve as partition walls separating the cotyledons, divide and branch repeatedly, penetrating deep into the fœtal part, though they do not reach the innermost portion, a fact that Kölliker had previously emphasized. No direct passage of these processes into fœtal

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* *Entwickelungsgeschichte*, 1861.

† *Sitzb. d. K. Akademie d. Wissenschaft.* Mai-Heft. Wien, 1868.

‡ *Icon. Phys.* Erkl. d. Taf. xxviii.

§ *Mikrosk. Unters. d. Blutgefässe des Muttertheils der Placenta. Medicinsky Westnik*, 1864, No. 13.

‖ *Zur Lehre über die Structur der Placenta.* Virch. *Archiv*, Octob.-Heft, 1867.

tissue takes place, but they end at the periphery of the cotyledons; consequently between the tufts of the central parts of the secondary cotyledons we never meet with maternal tissue. The more minute divisions of these tufts have the appearance of fibrillated tissue, and we rarely encounter in them the cell-elements of the uterine placenta.

As to the relations of the blood-vessels in the matured afterbirth, the researches of Kölliker, Virchow,* and others have shown that between the arteries and veins of this substance no capillary mesh-work exists, but that these vessels communicate with one another by means of sinuous intermediate spaces. These vascular spaces—which exist throughout the whole fœtal placenta, and also freely extend into the fœtal villi—are bordered by placental tissue only.

The existence of a delicate membrane, that E. H. Weber† first described as enveloping these vascular spaces of the maternal portion, later researches (Kölliker, Bidder‡) have not corroborated.

The placenta fœtalis, or fœtal part, is formed by the development of the villi of the chorion, in which branches of the embryonic umbilical vein and two umbilical arteries ramify.

A short time since, Jassinski devoted himself to a more careful study of the placental villi. He confirms the statement that the villi are invested with pavement epithelium, but states that the pavement layer may also receive a covering of columnar epithelium.

Since the tufts grow into the uterine follicles, their columnar epithelium may remain adhering to the isolated tufts. As to the proper covering of these villi, my researches have demonstrated the following: there are tufts bearing columnar epithelium; in such cases, however, there is no other epithelial coat to be met with; the columnar epithelium fringes the substance of the villus which bears the blood-vessel. The young tufts, on the other hand, are not covered with either columnar or pavement cells; at any rate the cell-bodies are not defined, but consist simply of protoplasma with numerous nuclei embedded in them. It is known that the tufts bud, and this process means that processes or nodules of protoplasm are emitted from the substance of each villus. These processes or projections become thicker and longer, and nuclei collect in them; we never encounter, however, a demonstrable cell-group, but only an aggregated mass of protoplasm. At a later stage we find a hollow space in the tufts, but even then, with the assistance of silver to color our preparation, we are unable to perceive the outlines of epithelial cells.

Soon, however, a mantle of columnar cells will be formed out of the mass of protoplasm with its embedded nuclei. We comprehend the histological condition by studying the successive stages of development.

We encounter, at first, solid villi, filiform in character; subsequently they are stouter; at a further stage the nuclei are abundant; then we notice some are hollow in the interior, and finally many that are hollow and bear columnar epithelium only.

I must allude here to the fact that I have repeatedly seen the outer border of the villi raised up and isolated from the basis substance; Goodsir §

* *Ueber die Bildung der Placenta*, 1853. *Gesammelte Abhandlungen zur Wissenschaftl. Medicin.*

† R. Wagner, *Phys.* 3 Aufl.

‡ *Zur Histol. der Nachgeburt.* Holst's *Beitrag zur Gynäcol. u. Geburtsk.* 1867, Heft 2.

§ *Anat. and pathol. Researches*, Edinb. 1845.

and Schröder van der Kolk * regarded this as an independent membrane. In these same cases I observed the nuclei were often separated from the border by a more or less considerable quantity of basis substance. I do not know whether the limiting membrane exists during life. Examination of fresh specimens with the best objetcives does not demonstrate any double contours. The membrane that after maceration by Jassinski's method in muriatic acid is found partially separated, can be the result of coagulation in the superficial portion of the protoplasm. Besides, it is not probable that a membrane forms itself on budding protoplasmic processes, since we afterwards find the outlines of cells lying free upon the surface.

The vessels of the villi do not lie immediately upon the wall of the villus, but they float, as it were, in an interspace of the villus, which we may also call a perivascular space. It is usually largest on the ends or in the buds of the villi, where the vessels enter but a short distance.

Schröder van der Kolk was the first to demonstrate that the arteries and veins of the villi not only communicate with one another by simple loops, but also form a rich capillary network.

The connective tissue of the chorion, too, as it grows, accompanies the vessels into the interior of the villus. In the trunks the connective tissue (Virchow's mucous tissue) shows a distinctly fibrillated structure; in the extremities it appears like a structureless intercellular substance, and no longer exhibits a fibrous texture.

Embedded in this villous tissue are round, spindle, and star-shaped cells, which are regarded by Kölliker as formation cells of connective tissue; in addition there are nuclei about which no cell-body can be discovered. This villous tissue passes directly into the connective-tissue basis of the chorion.

Between the chorion and amnion there is also a glutinous tissue, the so-called membrana intermedia; it represents, according to the researches of Bischoff † (Kölliker, Bidder), the residue of the fluid originally lying between chorion and amnion. There are no cell-elements or vessels in this glutinous layer.

III.—The Fallopian Tube.

[This article is contributed by Grünewald, a student of medicine, who acted under my direction in carrying out the necessary researches.—Stricker.]

The Fallopian Tube (Tuba or oviduct).—In the Human species the Fallopian tube springs from the superior lateral border of the uterus, behind and somewhat above the origin of the ligamentum teres uteri.

As to its course, it lies in the superior free border of the ligamentum latum, which serves as a mesentery for it.‡ It is partly straight and partly tortuous. The straight portion or isthmus (Barkow) lies nearer the uterus than the tortuous part or ampulla (Henle).

In Mammals the course pursued is different: with them the tubes may either continue tortuous, almost from their very commencement at the uterus, and not become straight until they approach the ovary, or the reverse may be the case. Sometimes they run the whole distance in small spirals, or they seem coiled in a knot and intertwined in one another as in the Rat

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* *Waarnemingen over het Maaksel van de menschliske Placenta en over haren Bloeds omlook.* Amsterdam, 1851.

† *Beitrag zur Lehre von den Eihüllen des menschl. Fœtus*, 1834.

‡ *Lehrbuch der Anatomie.* 2. Theil.

(Meyerstein*), the Simia Silvanus, and more particularly in the Opossum. (Blumenbach, *vergleichende Anatomie*, p. 486.)

The tubes are not always of the same length; at one time the right is longer, at another time the left. The isthmus is always shorter than the ampulla, though the relation of length between the two is different in different animals. In the common Fowl there exists but one Fallopian tube, and that is upon the left side, and this, indeed, is true of almost all Birds.

In the common Fowl, too, we find uniformly a furrow between the ovary and the tube; originally there are the rudiments of double female sexual organs; during the progress of development, however, the imperfect organ on the right side disappears.† The left tube descends more or less tortuously in front of the left kidney to the cloaca. At the lowest part it suddenly widens, and becomes the receptacle of the egg or uterus. It is attached to a fold of peritonæum.

Among the Amphibians the oviduct is double. In the Buffo cinereus it extends up over the root of the lungs; at this point the abdominal end is attached for about eight to ten lines, by means of a peritoneal fold, to the posterior abdominal wall. The upper part is very tortuous. The inferior end becomes suddenly wider and ends in a vesicular pouch, leading afterwards into the cloaca.

In the Human species and Mammals the oviduct communicates with the cavity of the uterus through the ostium uterinum. The opening is in the superior angle of the Human uterus, and is so narrow that a fine bristle can scarcely be pushed through it. The nearer, however, the canal approaches the external extremity, or ostium abdominale, the more it enlarges, until on reaching the outlet it again diminishes in size. Haller asserted that after the tube enlarged it became constricted again somewhere about the middle; Weber ‡ says the same thing. Meckel § computes the width of the ostium uterinum at half a line, the width of the ostium abdominale at from three to four lines. Krause ‖ estimates the width of the ostium uterinum at from one-fifth to one-fourth of a line, and the widest part, before reaching the ostium abdominale, at two lines. Huschke¶ thinks this last measurement may be as much as three or four lines.

In the Human female the oviduct enlarges and becomes funnel-shaped at its abdominal end. This part, the infundibulum, is separated by deep, radiating divisions into a number of lobes or fringes (fimbriæ), some of which are pointed, others are round. On the inner surface of these lobes are ridges, partly transverse, partly longitudinal, continuations of the mucous coat of the ampulla, and which cannot be smoothed out. One fimbria in particular surpasses the others in length. This is the so-called fimbria ovarica of Henle, which is attached with its peritoneal surface to the sharp and free border of the ligamentum infundibulo-ovaricum (Henle), a secondary fold of the ligamentum latum, lying between the lateral margin of the ovary and the infundibulum. This fimbria may reach as far as the top of the ovary, where its peritoneal investment is interwoven with the albuginea of that organ. Frequently, however, it extends only to the ovary, and in such cases the ligamentum infund. ovar. forms a furrow. In those instances in which a space exists between the fimbria ovarica and the ovarium, it

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* Henle und Pfeifer's *Zeitschrift*, 3. Reihe, Bd. 23, S. 63. *Ueber die Eileiter einiger Säugethiere.*

† Stannius, *Lehrbuch der vergleichend. Anatomie der Wirbelthiere*, p. 333.

‡ Bd. III. p. 616.

§ Bd. IV. p. 516.

‖ Bd. I. p. 559.

¶ P. 470.

is said that the intermediate sharp and naked border of the peritoneal fold is provided with ciliated epithelium. As for the ostium abdominale of the four Fowls that I examined, there was a double relation existing; in three cases the tube terminated in a blind extremity, and was provided at the end with an oblique opening, which led into a funnel with delicate walls: this opening lay in the above-mentioned furrow; and yet these were young animals that had not yet laid eggs.

The fourth case examined was an old Hen; and in her the ostium abdominale was funnel-shaped, almost as in the Human species.

In the Buffo cinereus the abdominal opening is attached at its upper extremity, and lies in a transverse fold of the peritonæum and shows the same relation as in the young Fowls.

In the Human Female, and in Mammals, if we divide the isthmus of the tube by a transverse incision, the lumen appears stellate. The following layers can then be distinguished in a direction from without inwards:—

1. The adventitia, exceedingly rich in vessels and connective tissue.

2. The muscular layer, consisting in great measure of circular muscular fibres; longitudinal muscular fibres are, however, embedded in it to a more or less degree.

3. Finally, the mucous membrane, which makes numerous folds, some of which are ovate, others are spherical, or simply form low ridges. A vibrating columnar epithelium of considerable height covers these folds; the interior is filled with a dense fibrillary network, rich in vessels. The muscular layer of the mucous coat consists of longitudinal muscles.

In the ampulla, the adventitia and muscular layers preserve the same relations. The mucous membrane differs, however, as may readily be imagined from the fact that its functions are not the same; it possesses much more complicated folds than the isthmus, and they project further into the passage, and frequently seem to be united with others on the opposite side; though a close examination generally shows that this is an apparent and not an actual observation, still such an attachment really occurs in some instances. These rugæ have usually subordinate or accessory folds, which in turn have also secondary ridges, so that they present on the whole the appearance of a branching tree. There are, too, unbranched folds arranged in close rows, which some authors (Bowman, Hennig) have been bold enough to ascribe to the mucous glands of the Fallopian tube. But we only have to make a thin longitudinal section of the tube, either in Man or Mammals, to be immediately convinced that no glands at all exist in the oviduct.

As for the more delicate structure of the fimbriæ, we find the same elements as in the other parts of the Fallopian tubes, of which they must be regarded as the immediate continuations. These fringes are very rich in blood-vessels.

In the Fowl the external covering and layer of circular muscular fibres are arranged just as in the Human species. The rugæ of the mucous membrane, which are longitudinal the whole length of the Fallopian tube, are unbranched, and consist of a finely fibrillated net-like tissue, in which round cells are generally embedded; these increase in size as you approach the epithelium. In the middle of the fold there is a highly vascular band of connective tissue, which sends off filaments in all directions into the fold, and thus the finely fibrillated network just mentioned is constituted. Along the top of the fold nothing more is to be seen of the cord of connective tissue, since at this point it is already exhausted by the distribution of branches into the interior. The epithelium is cylindrical and vibrating, and is ar-

ranged in several layers. The folds are at one time longer, at another shorter. The structure of the tube in the Buffo is entirely different. While we nowhere encounter glands in the oviduct of Mammals and Birds, we find throughout the whole length of the duct in this particular species (only excepting the upper attached part) glandular *bodies*. They are arranged at right angles to the long axis, and are only separated from one another by delicate connective tissue. If we spread out the mucous coat with needles, and examine it with even a lens of low magnifying power, we observe a fine velvety tissue between the longitudinal folds. The entire canal exhibits these folds, but they are highest in the neighborhood of the ostium abdominale. This tissue is only absent at the attached abdominal end, where the glands occur less frequently; it has minute openings, and presents in general a honeycombed appearance.

On transverse section we see, externally, an enveloping membrane of connective tissue; within comes a delicate layer of circular muscular tissue, upon which the mucous coat lies and in which the follicles are embedded; as already stated, fine filaments of connective tissue, derived from the mucous membrane and supporting the blood-vessels, are the only substance intervening between the follicles.

The mucous membrane is raised into numerous longitudinal folds, between which the orifices of the glandular tubes can be distinguished. These follicles are invested internally with well-defined pavement cells. The mucous folds are pretty high at the abdominal end, and divide into numerous branches, as in the Human female.

The interior is filled up with a dense cord of connective tissue, in which there are blood-vessels and some smooth muscular elements. The external investment consists of high cylindrical epithelium, with vibrating cilia. Throughout the remainder of the tube the folds are not branched.

CHAPTER XXXI.

THE SPINAL CORD.

By J. GERLACH,

OF ERLANGEN.

THAT portion of the central nervous system occupying the greater part of the spinal canal, called the spinal cord, constitutes a column mainly made up of nervous tissue, which in adults terminates on a level with the first lum-

Fig. 240.

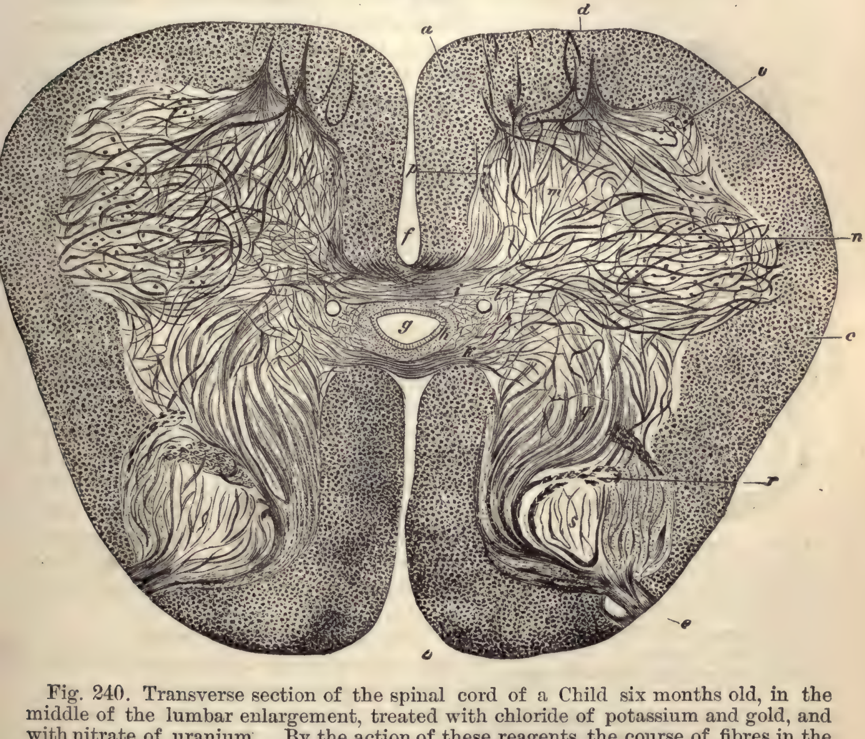

Fig. 240. Transverse section of the spinal cord of a Child six months old, in the middle of the lumbar enlargement, treated with chloride of potassium and gold, and with nitrate of uranium. By the action of these reagents the course of fibres in the gray matter is rendered unusually distinct. Magnified twenty diameters. *a*, anterior columns; *b*, posterior columns; *c*, lateral columns; *d*, anterior roots; *e*, posterior roots; *f*, anterior white commissure in communication with the anterior horns and columns; *g*, central canal lined with epithelium; *h*, connective tissue round about central canal; *i*, transverse fibres of the gray commissure lying in front of the central canal; *k*, transverse fibres of the gray commissure lying behind the central canal; *l*, cross-section of the two central veins; *m*, anterior horns; *n*, great lateral cell-group of anterior horn; *o*, smaller anterior cell-group; *p*, smallest median cell-group; *q*, posterior horns; *r*, ascending fibres in posterior horn; *s*, gelatinous substance.

bar vertebra by a conical extremity. This column, which exhibits an increase in thickness at the parts whence originate the nerves for the upper and lower extremities, the so-called cervical and lumbar enlargements, consists of two substances, of which the peripheral is white, the central gray.

Fig. 241.

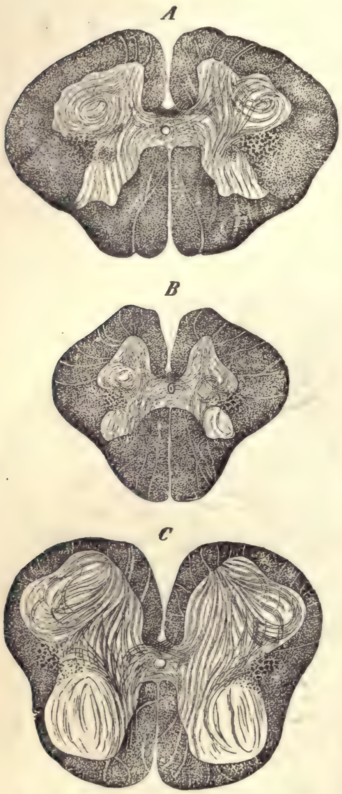

Fig. 241. Transverse sections of the spinal cord of a Child six months old, at various levels. Magnified 8 diam. *A*, From the middle of the cervical enlargement. *B*, From the middle of the dorsal region. *C*, From the middle of the lumbar enlargement.

The external white substance has for a long time been considered as separable in three pairs of columns, the boundaries of these being the anterior longitudinal fissure, the points of exit of the anterior and posterior roots of nerves, and the posterior longitudinal fissure. This division into anterior, lateral, and posterior columns, is tolerably distinct upon the surface of the cord, but is lost if the parts nearer the gray centre be examined. In addition to these six columns, in later years the anterior white commissure which lies in front of the gray commissure, at the base of the anterior fissure, has been considered as part of the white substance.

On a transverse section the central gray matter of the cord appears in the well-known form of a capital Latin H, the two lateral parts having between them the posterior commissure and the central canal (fig. 240, *i g k*); the anterior part of the limbs of the H being called the anterior horns (fig. 240, *m*), the posterior half the posterior horns (fig. 240, *q*).

These lateral portions vary much in outline, as seen by comparing sections taken from different parts of the cord; but even when presenting the greatest differences, which are met with in the cervical and lumbar enlargement, still retain the original form of a capital letter H, which in the dorsal region appears composed of narrow side pieces, in the cervical and lumbar regions of broad ones (fig. 241, *A B C*).

A knowledge of the relative proportions of the white and gray substances is of the highest importance for a proper understanding of the spinal cord. This is by no means uniform in various parts of the organ, but, on the contrary, very variable. By the comparative study of transverse sections made at different levels in the cord, the observer very soon becomes aware of the fact that the enlargements in the cervical and lumbar regions are solely due to increase of the gray matter.

The comparison of such sections furthermore teaches that the white substance, gradually, it is true, but unmistakably increases in amount from below upward, as is shown in the most convincing manner by the annexed drawings (fig. 241), made with photographic exactness from sections of the Human spinal cord in the cervical, dorsal, and lumbar regions. In the

decreasing *conus medullaris* the white substance rapidly diminishes as compared with the gray, and, finally, at the termination of the cord in the *filum terminale*, the white substance altogether disappears. The white substance of the spinal cord contains as nervous elements large and medium-sized nerve-fibres, as well as connective tissue and blood-vessels; the gray matter, besides large, frequently dividing nerve fibres, presents the finest fibrillar elements with which I am acquainted in the nervous system, the disposition of which in the shape of a network in combination with nerve-cells constitutes the distinctive character of the gray substance, as contrasted with the white.* As regards other than nervous elements, we here meet with blood-vessels, much more numerous than in the white substance, and whose capillaries form an exceedingly fine network; epithelium lining the central canal; and connective tissue, which last is particularly abundant in the immediate neighborhood of the central canal, and in that portion of the posterior horns known as the *substantia gelatinosa* of Rolando.

The White Substance of the Spinal Cord.

The white substance of the spinal cord is surrounded by a layer of connective tissue, a dependence of the pia mater. This layer remains clinging to the cord after the removal of the pia mater, which comes away from the cords of Infants or young subjects in the shape of long shreds, by careful pulling from above downward. The cause of the phenomenon is partly that this layer is united by continuity with the connective tissue of the cord, partly that the fibrillation of the connective tissue which constitutes the separable part of the pia mater has an essentially longitudinal direction, whereas the layer adherent to the cord is made up of connective tissue whose fibres are mainly disposed in a circular manner. The longitudinal tissue of the separable pia mater is, however, continuous with the adherent layer of circular fibres. It depends upon the greater or lesser closeness of this union, whether the pia mater be easily or with difficulty stripped off.†

Both portions of the pia mater extend to the bottom of the anterior fissure, that is to say, as far inward as the anterior white commissure, while only the adherent layer of the pia mater sinks directly down into the posterior fissure to the gray commissure. This posterior septum unites the posterior columns so closely that a posterior fissure cannot well be said to exist, in the strict meaning of the word. In this manner the anatomical dispute about the existence of a posterior fissure finds a solution.

The posterior septum is not the only process of the peripheral connective tissue penetrating the interior of the spinal cord, but there are seen, in transverse sections, very numerous similar septa which traverse the white substance, reaching the gray, and uniting among themselves in the most complicated manner. The difference between these septa, which start from

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* In the dorsal region of the Human spinal cord there are also found a few small, scattered nerve-cells in the connective-tissue trabeculæ of those portions of the lateral columns which lie next the gray matter. In the marrow of the Ox and Sheep these cells are much more abundant.

† How easily this formless connective tissue is sometimes torn I observed in the body of a Child sent me many years ago as a curiosity from a neighboring town, with the remark that it was an instance of a spinal cord without a single attached nerve. The spinal canal was unopened, but the entire well-preserved spinal cord had already been removed, of course deprived of pia mater and nerve roots, and was separately wrapped up. In this exceedingly rare case it had accidentally been possible to extract the entire spinal cord from the spinal canal by a pull from above, while the pia mater and the external membranes with the nerve-roots remained behind in the spinal canal.

every part of the periphery of the cord, and the posterior septum, is that the latter extends directly down to the gray matter, whereas the former branch and join like the veins of a leaf, and follow no direct course. We are consequently led to look upon the connective tissue of the white substance as a network of large and small bundles, in whose meshes longitudinally arranged nerve-fibres are imprisoned. The course of the blood-vessels coincides with that of the connective-tissue bundles. The size of these bundles is easily ascertained by the diameter they present in transverse sections. The largest, those immediately derived from the peripheral connective-tissue layer, measure from .015 to .02 mm., and by repeated division decrease to .008 mm. The superficial area of the more or less rhombic spaces enclosed by these bundles measures on transverse sections from .03 to .09 square mm.

This layer at the circumference of the spinal cord, as well as the network of trabeculæ proceeding from it, possesses a peculiar structure, which has occasioned the creating of a special tissue, the so-called nerve-cement or neuroglia. The external, thicker part of the peripheral layer, and a large proportion of the septa starting from it, exhibit the well-known structure of fibrillar connective tissue, consisting of undulating bundles of fine connective-tissue fibrillæ, which run horizontally to the vertical axis of the body. After the addition of alkalies, by which these fibrillæ are made to disappear, a few elastic fibres may be perceived. In chromic acid preparations which have been stained by a solution of carmine, there are also seen, best after the action of very dilute acetic acid, cellular elements with highly-colored nuclei, and a varying number of processes, some branching, which can be isolated with comparative ease in consequence of the prolonged action of the chromic preparation.

In the immediate neighborhood of the spaces above referred to, the microscopical appearance of the tissue changes. The fibrillæ disappear, and in their stead is seen a very finely granular substance which is continuous with the fibrillar tissue, and extends into the spaces of the fibrous network, filling these in such a way as to leave room only for the passage of nerve-fibres, which nearly all proceed vertically; a disposition which is best seen in the thinnest possible transverse sections. In such preparations are seen transverse sections of nerve-fibres, closely surrounded by this finely granular substance, and in some places round apertures are perceived, from within which the cut nerve-fibres have escaped (fig. 242, *B c*). This finely granular substance is traversed in all directions by extremely delicate fibres, which are joined to one another in the most complicated manner (fig. 242, *A a*). This microscopic appearance of the granular substance, with its contained network of fine fibres, only distinctly seen in the thinnest cuts, bears the greatest resemblance to the fundamental substance of yellow or fibro-cartilage, as, for example, that which is found in the arytenoid cartilage of the Ox. Opinions are divided touching the histological significance of this web of fine fibres. Kölliker * considers it as a network of stellate cells, presenting this peculiarity, that their processes repeatedly branch and communicate with each other and with neighboring cells. Henle and Merkel † insist upon the resemblance of this network to a reticulation of fine elastic lamellæ; while, on account of their dimensions, their powers of refraction, and their chemical characteristics, ranking the bundles of fibres with connective-tissue fibrillæ. I cannot accept either of these views, but consider the net-

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* Kölliker, *Handbuch der Gewebelehre.* Fünfte Auflage, S. 267. French edition, Vol. I. Paris, 1869, p. 349 et seq.

† In *Zeitschrift für rationelle Medicin.* Dritte Reihe, Bd. 24, S. 56.

work as belonging to the elastic tissues, to which opinion I am led, as well by the resemblance of the tissue with the fundamental substance of elastic or fibro-cartilage, as by the resistance which these fibres, like elastic fibres, oppose for a certain length of time to the action of alkalies.

Fig. 242.

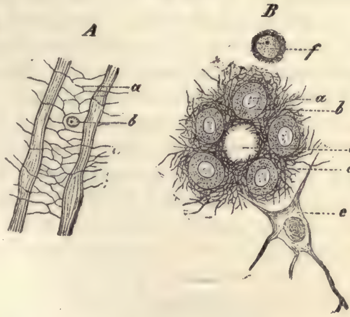

Fig. 242. *A*, Longitudinal section of the white substance of the Human spinal cord. *a*, elastic fibres of the connective substance; *b*, cellular element of the connective substance. *B*, Transverse section of the white substance. *a*, axis cylinder; *b*, myeline; *c*, aperture from within which a transversely cut nerve-fibre has fallen; *d*, finely granular connective substance, containing delicate elastic fibres; *e*, full-grown connective-tissue cell, with processes; *f*, young connective-tissue cell, whose nucleus is surrounded only by a small amount of protoplasma. Magnified 300 diam.

Besides the reticulum of elastic fibres, we find cellular elements in the granular substance. These are more or less abundant in various parts of the spinal cord, and exhibit a variety of transition shapes, from such as consist of a very small amount of protoplasma round about a nucleus (fig. 242, *B f*), to the completely developed connective-tissue cell having processes (fig. 242, *B e*). By the prolonged action of a very dilute ammoniacal solution of carmine, these cells become tinged in accordance with the staining law of dead tissues; the nucleus of the deepest hue, the protoplasma, and the processes likewise, when present, less deeply but still distinctly; whilst the delicate network takes up no coloring matter whatever, a fact which affords no little support to my opinion, that this network belongs to the elastic tissues; since it is well known that elastic fibres are completely indifferent to the action of ammoniacal carmine.

As already stated, nothing is to be seen in the tissue immediately surrounding the nerve fibres, as well as in the neuroglia existing in the gray substance of the cord, but a peculiar modified connective tissue, whose semi-solid fundamental substance is finely granular and fibrillated; or, according to Walther's* observations on the frozen living brain, which need confirmation, only a structureless tissue. If the latter view be exact, the finely granular state of the neuroglia must be looked upon as produced by the prolonged action of hardening solutions. This finely granular or primitively structureless fundamental substance, as is not unfrequently the case in ordinary fibrillar connective tissue (serous membranes, for example), is traversed in all directions by a network of delicate elastic fibres containing cellular elements, connective-tissue corpuscles in various stages of development. As regards the origin of the latter elements, Henle and Merkel,† starting from the well-known observations of Cohnheim on suppuration, have advanced an interesting hypothesis to the effect that these cellular elements are nothing but exuded white blood corpuscles.

The nerve fibres of the white substance possess an essential part, the axis cylinder, whose diameter bears a tolerably constant relation to that of the nerve fibre itself, measuring from one-fourth to one-third the width of the latter. In preparations slightly hardened by chromic salts, after the action of alkalies, a finely striated structure of the axis cylinder is unmistakably

* Walther, *Medic. Centralblatt*, Jahrg. 1868. S. 450. † Loco cit. S. 79.

visible with the higher powers; and I indorse, as regards the intimate structure of the axis cylinder, the excellent description given of it in this work by M. Schultze.* A second constituent part of nerve fibres, hardly ever wanting in fully developed ones, is the nerve marrow or myeline, for an account of whose histological and micro-chemical characters I again refer to M. Schultze's article. In thin transverse sections of the cord, after coloring with ammoniacal carmine, the distinction between the axis cylinder and the myeline appears most striking. Each nerve fibre then exhibits the well-known almanac representation of the sun, in the centre being a large dot of an intense red color, surrounded by a broad, refracting ring of myeline (fig. 242 *B a b*). Not unfrequently, in cross-sections, the myeline presents a more or less marked concentric lamellation. Whether this is to be considered as a peculiar effect of coagulation, or as the expression of a really concentric disposition around the axis cylinder, I dare not decide.

It is denied that the sheath of Schwann (neurilemma) which surrounds the medullated peripheral fibres, exists upon those of the central organs. In fact no trace of this sheath is visible upon an isolated fibre of the gray or white substance. It is, however, possible that it is not wholly wanting, being invisible in teased preparations because of its intimate union with the neuroglia. One thing favorable to this view is that in transverse sections of the white substance the limit between the myeline and the neuroglia is indicated by a sharply defined line, which may be accepted as evidence of the presence of a membrane of Schwann. The following facts still further support this opinion: that by its micro-chemical reactions, the membrane of Schwann is known to belong to the elastic tissues, and that the delicate elastic fibres, demonstrated by me in the neuroglia, can be followed close up to the limit of the myeline, and, as may be well seen in a thin, slightly compressed longitudinal section, often terminate by sharply-cut ends (fig. 242 *A*). Since it can neither be maintained that there is a continuity between the elastic fibre and the myeline, nor that there is any difference in chemical constitution between the membrane of Schwann and the elastic fibres, it is not very hazardous to conclude that the elastic fibres coalesce with the equally elastic sheath of Schwann developed from the neuroglia. Considered from this point of view, the existence of a network of elastic fibres has an unmistakable physiological significance, appearing to be a preservative medium intended to protect the nervous elements in the stretching and twisting to which the spinal cord is subjected by reason of the movements of the vertebræ. I have not been able satisfactorily to observe divisions of nerve fibres in the white substance, but other observers† claim to have seen this in fine fibres.

The diameter of nerve fibres in the white substance is not at all uniform, as is shown by the comparison of the size of fibres in various parts of cross-sections of the cord. The thickest fibres, measuring from .012 to .02 mm., are found in those portions of the anterior columns which form the edges of the anterior median fissure. This is also the part in which the difference in breadth between fibres enclosed in one compartment of the neuroglia is the least striking. In the lateral columns, in the same compartment, we meet with fibres .014 or .018 mm. in diameter lying close to others which only measure .004, .006, or .008 mm. In the peripheral meshes broad fibres predominate, while in those nearest the gray matter the smallest are observed. In the posterior columns there is a certain regular gradation in the diameter of

* S. 118.

† O. Deiters, *Untersuchungen über Gehirn und Rückenmark*, herausgegeben von Max Schultze. Braunschweig. 1868. S. 110.

fibres, which increase in thickness from behind forward, that is to say, as we observe them nearer to the posterior gray commissure. In the last-named part the fibres of the posterior columns have a diameter of .014 mm., while those lying further back become more and more slender, reaching .005 and .008 mm. In the upper dorsal and in the entire cervical regions there is found, separated by a strong fibrous septum from the posterior columns, and placed against each side of the median line, a bundle * of small fibres, which bundles resemble wedges in cross-sections, whose apices look forward and inward, and whose bases are directed backward (compare fig. 241 *A*). In the spinal cord of animals the variations in the diameter of nerve fibres are much greater than in Man, and the greatest extremes are met with in the cords of the lowest Vertebrata.

Fig. 243.

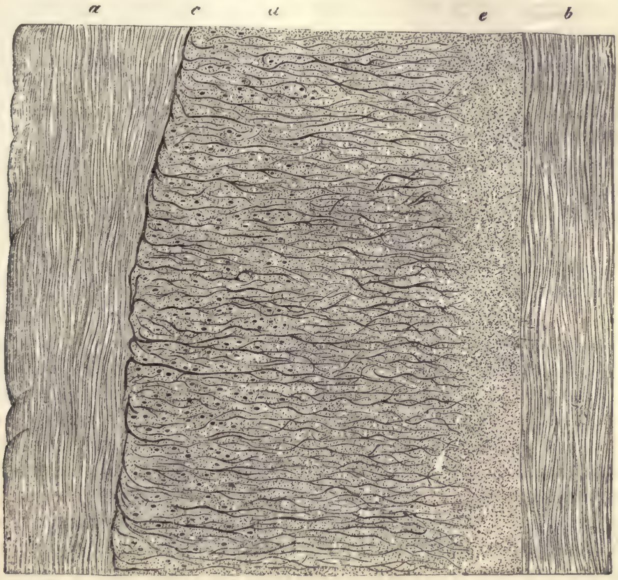

Fig. 243. Longitudinal section of one-half of the spinal cord, made from right to left in the middle of the anterior horn, in the lumbar enlargement of the Human cord; treated with chloride of palladium, and chloride of gold and potassium, by which the fibrillation, particularly that in the lateral portion of the gray substance, is brought out with extraordinary sharpness. Magnified 50 diam. *a*, lateral column; *b*, anterior column; *c*, entrance of the fibres of the anterior horn into the lateral column, preparatory to ascending in these; *d*, lateral part of the anterior horn, showing fibres and the cells of the lateral groups; *e*, internal part of the anterior horn.

As regards the relative proportion between nerve fibres and connective-tissue neuroglia, as far as this can be appreciated in transverse sections, they appear about equally abundant in the anterior and lateral columns; only in

* These are the parts of the posterior columns which were first described by Burdach as *slender columns*, and which Kölliker called columns of Goll; a name, it seems to us, not very fortunately chosen, because Burdach divided the posterior columns in the cervical region into slender columns (columns of Goll) and cuneiform columns, by the latter term meaning the remaining lateral portions of the posterior columns of the cervical region, after the separation of the median slender bundles.

that portion of the lateral columns which borders on the gray matter, connective-tissue predominates. The posterior columns seem richer in neuroglia than the antero-lateral columns; and especially is this true of the median subdivision of the posterior columns, the columns of Goll, cuneiform columns, or slender columns of Burdach, which, in successful carmine preparations, consequently appear of a deeper red than the circumjacent parts of white substance.

As regards direction, we distinguish in the white substance of the spinal cord, vertical, horizontal, and oblique fibres.

By far the most numerous are the vertical fibres which constitute the principal part of the columns of the cord, and which, united in thick or thin bundles, proceed upward in a parallel course to the medulla oblongata. The demarcations between the different bundles of fibres are seen in transverse sections to consist in connective-tissue septa derived from the inner portion of the pia mater. It is by no means rare, in longitudinal sections, to see these bundles superimposed and interlaced; but, in my opinion, this apparent interlacing of bundles of fibres below the medulla oblongata is to be explained by the fact that it is extraordinarily difficult to obtain perfectly longitudinal sections of the spinal cord. The greater number of our so-called longitudinal cuts are in reality more or less oblique; and it is not surprising that in such we should mistake mere superposition of bundles for interlacing. I have been able to ascertain with certainty the occurrence of real interweaving, and the passage of fibres from one fasciculus to another, only in the internal portion of the lateral columns.

Horizontally disposed fibres are found in the following parts of the white substance of the spinal cord:—

1. In the anterior white commissure, where the horizontal course of the fibres is easily demonstrated in transverse sections. They here appear in the shape of an exquisite crossing (fig. 240 *f* and fig. 249 *i*), which must not, however, be taken as proof of the decussation of the anterior columns. On the contrary, according to my observation, all the horizontal fibres of the anterior white commissure which pass over to the opposite side to go on up toward the brain, spring from the gray substance of the anterior horn in such a way that fibres coming from the right anterior horn ascend in the left anterior column, and those derived from the left anterior horn ascend in the right anterior column (fig. 249). In order to take this course the fibres must necessarily cross the median line, and the place where this happens is the anterior white commissure.

This view is favored by the circumstance that the anterior white commissure is broadest in those parts of the spinal cord where the gray substance is most abundant, and narrowest where it diminishes.

2. The second place in which horizontal fibres make their appearance is in the internal parts of the lateral columns which border on the gray substance (fig. 243 *c*). These are the fibres which, proceeding laterally from the gray substance of the anterior horns, take an upward course in the lateral columns. At their point of exit from the gray matter, these fibres for a short distance follow a horizontal direction. Certain fibres of the posterior columns exhibit a similar arrangement, viz., those which are continuous with the fibres lying in front of the substantia gelatinosa (244 *g*). These take, for quite a distance in the posterior columns, a clearly horizontal course, as is well shown in transverse sections treated with chloride of gold. However, while in the case of the horizontal fibres of the lateral columns it seems pretty well established that they proceed from the gray matter into the lateral columns and ascend in these, as regards the horizontal fibres of

the posterior columns, it is not easy to determine whether they come from the gray matter of the posterior horn, to continue their course in the posterior column, or whether they do not belong to that portion of the posterior root fibres which, before entering the posterior horns, ascend or descend in a certain length of the posterior column, then turn in the posterior column and penetrate the gray substance of the posterior horn.

Fig. 244.

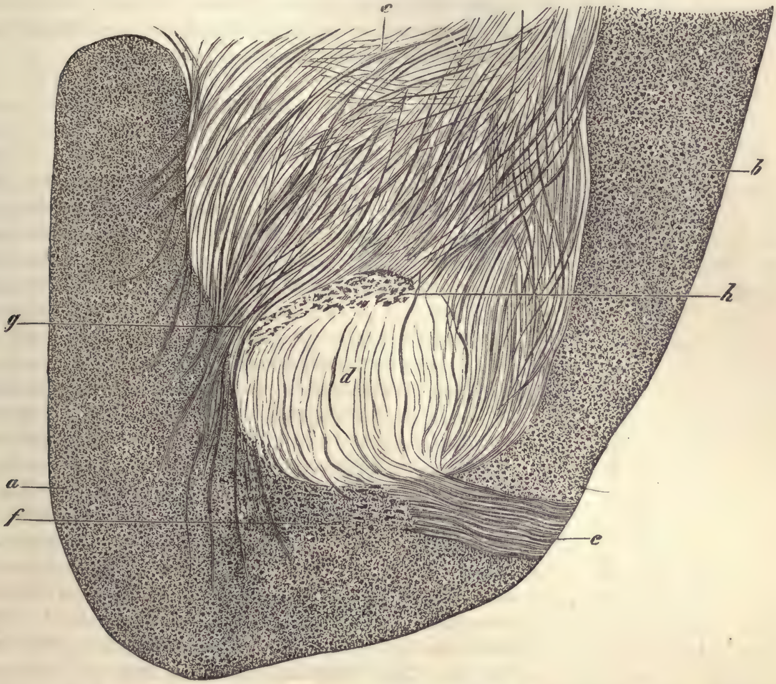

Fig. 244. Transverse section of the posterior half of the Human spinal cord in the lumbar enlargement, treated with chloride of gold and potassium, and showing unusually well the fibrillation of the posterior horn of the gray matter, magnified 50 diam. *a*, posterior column; *b*, lateral column; *c*, fibrillations of the posterior horn; *d*, substantia gelatinosa; *e*, posterior nerve root; *f*, fibres of the posterior roots, which ascend and probably also descend a certain distance in the posterior column before entering the gray matter; *g*, horizontal fibres, which pass from the posterior horn into the posterior column and *vice versâ*; *h*, fibres which lie in front of the substantia gelatinosa and ascend in the posterior horn.

3. The fibres of the posterior roots are also to be looked upon as constituting tolerably horizontal fibres of the white substance; nearly all of which proceed from without toward the median line (fig. 244 *c*), and consequently appear as transversely cut across in antero-posterior longitudinal sections (fig. 252 *g*). A part of the fibres belonging to the posterior roots certainly retain their horizontal course in the white substance, and enter directly into the substantia gelatinosa of the posterior horns; whereas the middle portions of these roots (fig. 244 *f*) turn up in that part of the posterior columns which borders on the substantia gelatinosa, therein take a vertical direction, ascending or perhaps descending in them for a longer or shorter distance,

previous to again turning to enter the gray substance lying just in front of the substantia gelatinosa (fig. 244 *g*).

The anterior roots contain the oblique fibres of the white substance of the spinal cord. On exactly transverse sections these fibres are only partially visible (fig. 240 *d*), whereas in antero-posterior longitudinal sections the obliquity of their course is plainly revealed (fig. 252 *b*). Oblique fibres are also met with in the upper part of the cervical region of the spinal cord, and much more abundantly in the medulla oblongata. These belong to the inner portion of the lateral columns, and proceed inward and forward; they are naught but the beginning of the pyramidal fasciculi, which attain their greatest development in the medulla oblongata.

The Gray Substance of the Spinal Cord.

In the gray, as in the white substance, the neuroglia is abundant. This constitutes the support for the nervous elements of the gray matter, and is continuous with the same tissue in the white substance. The posterior longitudinal septum, as well as the above-described septa of the white columns, lose their fibrillated structure after their entrance into the gray substance, and take on the histological characters of that tissue which we have studied, that forming the support of nerve fibres in the network of the white matter. This tissue (neuroglia) presents some peculiarities in the immediate neighborhood of the central canal, and in that portion of the posterior horns which bears the name of *substantia gelatinosa.* When we come to describe in detail particular portions of the gray matter, these peculiarities will be dwelt upon (fig. 245).

Fig. 245.

Fig. 245. A partially medullated nerve fibre, showing repeated subdivisions, isolated from the gray matter of the Human spinal cord treated with bichromate of potassa, magnified 300 diam.

The nerve fibres of the gray matter are extraordinarily abundant and constitute its greater part. Many bear myeline, very many show only a naked axis cylinder, upon which no myeline can be demonstrated. They are distinguished from the fibres of the white substance by the frequent divisions, which may be observed in a single fibre, and by means of which the diameter of the original nerve fibre is ultimately much reduced. Precise mensurations of these fibres are not easily made, because, below a size of .004—.005 mm. there are fibres of most varying diameters down to an immeasurable size, which last are by far the most numerous. These extremely fine fibres, resulting from repeated subdivisions, form a narrow-meshed network, which, together with nerve-cells, constitute the characteristics of the gray matter of the spinal cord. This network cannot be seen in absolutely fresh spinal cords, and even in cords treated by chromic salts, the action of other reagents is necessary to render it visible. As the gray matter is as yet so little understood, we may be allowed to speak briefly of the methods requisite for its study.

A certain degree of hardening of the spinal cord must precede the employment of one method, which essentially consists in the treatment of thin

sections by the chloride of gold and potassium. For this purpose (hardening) a solution (1 to 2 per cent.) of bichromate of ammonia is preferable to all other chromic preparations. Small fragments of perfectly fresh Children's cords, immersed in such a solution and kept in it in a cool place for fifteen or twenty days, attain a degree of consistency sufficient for cutting. The network of nerve fibres appears so much the more finely that the time necessary to hardening has been shorter. For the making of the thinnest possible cuts, which need not be entire transverse sections, I make use of Welker's microtome, as improved by me.* The sections are placed in a solution of 1 part chloride of gold and potassium and 10,000 parts of water very slightly acidulated with hydrochloric acid, and left in it ten or twelve hours, until stained of a pale lilac color. The sections are next washed in a solution consisting of 1 part hydrochloric acid to 2,000 or 3,000 parts of water, placed for 10 minutes in a mixture of 1,000 parts alcohol (60 per cent.) and 1 part hydrochloric acid, then transferred for a few minutes to absolute alcohol, after which they are to be rendered transparent by oil of cloves and mounted in Canada balsam. At first the network of fibres is not very distinct, but in the course of three or four hours it acquires great sharpness. Ultimately, if the gold solution has been too strong, or if the sections have lain too long in it, the fibres become almost black, which impairs the distinctness of the structure.

The second method (which has this advantage over the first, that by it we succeed in demonstrating the relation of the fibre network to the cells) consists in a peculiar use of ammoniacal carmine. As it is necessary to make use only of entirely fresh, warm spinal cords, we employ, by preference, those of the Ox or Calf. From these, with a razor, thin longitudinal sections are cut,† involving the anterior horns, and these sections are at once placed in an exceedingly weak solution of bichromate of ammonia (1 part to 5,000 or 10,000 of water), in which they are allowed to remain, in a cool temperature, for two or three days. They are then transferred to a very dilute solution of ammoniacal carmine, and in the course of 24 hours they assume the coloration necessary to further preparation. After washing with distilled water, the thinnest, and consequently best stained parts are teased apart with needles, under a low magnifying power, by which process the nerve cells, appearing as dark red points, are easily separated from the adherent portions of nervous matter. The preparation is then either mounted in glycerine, or, better still, the water being allowed to evaporate, the dried object, after the addition of one drop of oil of cloves, is embedded in Canada balsam.

Both these methods are of the highest importance for the study of the gray matter of the spinal cord, because by their use it is possible to distinguish the fibres of the neuroglia—which, though of similar dimensions, are stained neither by chloride of gold and potassium nor by ammoniacal carmine—from the true nerve fibres. From the network of nerve fibres there are developed thick fibres, which unite with still thicker fibres, and, traversing the gray matter, take their course through the white substance of the columns (figs. 249, 243, 244), or which conjoin with the medium-sized fibres of the posterior horns.

The nerve cells of the spinal cord are multipolar cellular bodies, without

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* J. Gerlach, "Zur Anatomie des menschlichen Rückenmarks," *Med. Central.* Jahrg. 1867. No. 24.

† The fresher the spinal cord the more easily are thin sections made, because the consistence of the cord diminishes rapidly after death.

Fig. 246.

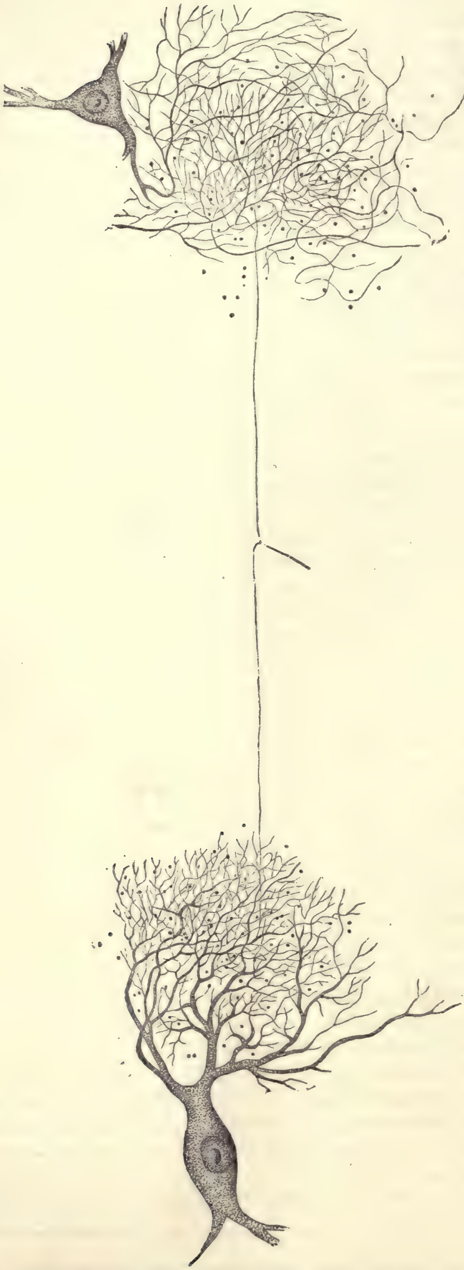

Fig. 246. A branching nerve fibre whose two branches are connected with the fibre network which is in relation with two nerve cells. Ammoniacal carmine preparation from the cord of the Ox, magnified 150 diam.

cell membranes; each cell is possessed of a large homogeneous nucleus, which itself encloses a nucleus, exceptionally provided with two vacuoles. Very commonly the cells contain pigment masses, composed of a large or small number of granules, and which are not unfrequently met with in the cell processes. These cells vary extraordinarily in shape and size, and below .12 mm. all intermediate dimensions are met with. The largest cells are found in the anterior horns, the smallest in the posterior, and those of medium diameter in that mass of cells which is restricted to the dorsal region of the spinal cord, lying to the side and a little back of the central canal, the columns of Clarke. While we possess in ammoniacal carmine and in chloride of gold and potassium two exquisite reagents, which enable us to distinguish the fibres of the neuroglia from true nerve fibres, we as yet lack the means of making an accurate diagnosis between nerve cells and the cellular elements of connective tissue; they are both stained alike by ammoniacal carmine, and chloride of gold and potassium have no action upon either. There is certainly no mistake possible as regards the large and the medium-sized cells, but even an expert observer may find it difficult to distinguish the smallest nerve cell from certain cellular elements of the neuroglia.

Very recently two important advances have been made in the morphology of the nerve cells of the spinal cord. One of these is Deiters' * discovery of the differences, in the processes of these cells; and the other, Max Schultze's † observations on the fibrillary appearance of the cell bodies and cell processes. For details concerning the latter, I can do no better than refer to p. 135 of this work; but Deiters' discovery demands a closer discussion, as it is of the greatest importance in connection with the origin of nerves in the spinal cord.

Deiters first noted the remarkable fact, that among the numerous processes which proceed from a cell, one always keeps on its course without division, whereas the others undergo frequent subdivision. This single process,‡ which either proceeds directly from the body of the cell, or springs from one of its first thick processes, is at its origin very slender, but gradually becomes thicker (figs. 247 and 248); this being the reason why the fibre breaks off with extraordinary facility near its junction with the cell during the making of the preparation; doubtless, the reason why attention was not drawn to it before. In chromic acid preparations the single process appears more homogeneous, while the branching processes present a fine granular appearance, but this difference between the two kinds of processes has lost its value since M. Schultze has demonstrated that in the fresh state both the single and the branching processes possess a fibrillated structure. At a varying distance from the nerve cell the single process appears surrounded by myeline, and so becomes a true central nerve fibre, having myeline and an axis cylinder, the latter being the undivided cell process itself. What becomes of this fibre evidently derived from a nerve cell, whether it ascends to the brain in the white columns, or whether it goes to form a part of the roots of spinal nerves, is not as yet clearly ascertained. Deiters assumed the latter view and called the fibre, "nerve process," while the branching prolongation he called by the perhaps even less happy name of "protoplasma processes," designations which we will retain, because they have become established.

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* Deiters, loco cit. S. 53.

† M. Schultze. *Observationes de structura cellularum fibrarumque nerveorum.* Bonn, 1868.

‡ I take the liberty of using the term *single process*, instead of the more correct one, *non-branching process.*—TRANSLATOR.

There are now three questions which present themselves to the unbiassed observer relative to these processes. 1st. What direction does the nerve process take, and what does it ultimately become? 2. What becomes of the protoplasma processes? 3. Do all nerve cells in the spinal cord possess nerve processes, or are there some which send out only protoplasma processes?

Fig. 247.

Fig. 247. A nerve cell from the anterior horn of the Human spinal cord. *a*, nerve-process; *b*, pigment granules. Magnified 150 diam.

As regards the first question, it was a decidedly fortunate idea of Deiters to connect the nerve process of cells with the origin of spinal nerves. Even if the relation be not as simple as Deiters thought, he holding that the fibres of the anterior roots sprang from the cells of the anterior horns, and the fibres of the posterior roots from the cells of the posterior horns, still it may be said with approximate certainty that Deiters hit upon the truth as regards the origin of the anterior roots. It is true that with our present means of investigation we cannot follow a nerve fibre belonging to an anterior root directly to a nerve-cell; yet transverse sections of the spinal cord treated with chloride of gold and potassium, and longitudinal cuts treated with ammo-

niacal carmine, now and then yield preparations which hardly allow of any other interpretation than that given by Deiters. Upon the former the bundles of fibres constituting the anterior roots may be seen entering the gray matter and taking their course in the direction of the cell groups of the anterior horns, near which they execute a curvilinear decussation. Fibres belonging to the anterior roots may be traced still further in the cell group; but their relation with the nerve cells escapes accurate observation, because chloride of gold and potassium has no effect upon nerve cells, and in such preparations as show the course of fibres in the most beautiful way by means of this reagent the cells are hardly to be seen at all. On the other hand, upon longitudinal sections of the Calf's spinal cord moderately hardened in bichromate of ammonia, thoroughly stained (in ammoniacal carmine) and well washed, it is possible, by means of gentle pressure, to observe nerve processes proceeding directly from certain cells, and to follow them for a part of their course. The direction taken by these nerve processes is always horizontally forward; while the many branched protoplasma processes run out in various directions. Even if I have been unable to follow one of these nerve processes into the anterior roots, their course in bundles toward the point of entrance of these roots, taken together with the fact that in the cervical and lumbar enlargements the increase in the root fibres co-exists with an increase in the number of cells, leads me to the belief that the nerve processes of cells must be considered as the beginning of the nerve fibres making up the anterior roots.

Much more difficult of investigation, and therefore much more obscure, are the conditions of origin of the posterior groups. In the posterior horns there are no more or less circumscribed cell groups, but the cells are scattered in among the nerve fibres, and are considerably smaller than those of the anterior horns; and besides, as already stated, we possess no means of distinguishing the smallest of these cells from the cellular elements of the neuroglia. It is true that Deiters has described nerve processes in cells apparently belonging to the posterior horns, but he has given no information concerning the course of these processes. I have also observed small cells provided with nerve processes lying behind the cell groups of the anterior horns, in that intermediate zone of gray matter which belongs neither to the anterior nor to the posterior horns; but I have seen, in longitudinal sections treated with ammoniacal carmine, that the nerve processes of these cells invariably proceed horizontally forward. Consequently these small cells, as well as the larger ones of the anterior horns, must be looked upon as sources of origin of the anterior root fibres. It is, moreover, to be borne in mind, that the number of genuine nerve cells in the posterior horns is smaller than that in the anterior, whereas the anatomical fact has long been known that the posterior roots are thicker than the anterior, and that they are made up of much more slender fibres. Consequently the number of nerve fibres which pass out of the spinal cord by way of the posterior roots is much larger than that of those which proceed with the anterior roots, and it appears very unlikely that the posterior nerve roots should have an origin similar to that of the anterior. On the contrary, that rich fasciculation of nerve fibres, which is met with in that part of the posterior horns which lies immediately in front of the *substantia gelatinosa*, seems to indicate that the posterior root fibres are not directly connected with nerve cells, but that they first enter into this network of nerve fibres in the gray matter, and that it is through them that the connection between the fibres of the posterior roots and nerve cells is established. If this view be correct (and in gold preparations appearances are often seen which seem to support it), a radical mor-

phological difference between the two physiologically different sets of nerve roots will have been discovered.

In answer to the second of the questions above stated, viz., that concerning the ultimate destiny of the protoplasma processes, we have an observation of Deiters, who sometimes saw the finest of these branches assume a dark-edged double contour, and in a few instances noted their further subdivision. Starting from these observations, Deiters considers these last branches of the protoplasma processes as none other than the axis cylinders of the finest nerve fibres, and looks upon these as a system of nervous links uniting the ganglionic cells among themselves. Had Deiters gone a step farther he would have been led to the discovery of the delicate network of nerve fibres in the gray substance; but as he did not make use of ammoniacal carmine in the making of his dilacerated preparations, and as he knew nothing of the gold method, the nerve fibre network remained concealed from him. I can not only corroborate Deiters' observation, but must go farther, and state it as my opinion that the finest branches of the protoplasma processes subdivide so as ultimately to constitute that delicate nerve fibre network which I consider as an essential constituent of the gray matter (see fig. 246). The divisions of the protoplasma processes surrounded by a dark-edged double contour seen by Deiters, are nothing but the beginning of the fibres of this network. Accordingly the cells of the gray substance provided with nerve and protoplasma processes are united in two ways with the fibrillated nervous elements of the spinal cord; first, by means of the nerve processes which become the axis cylinders of anterior root nerves, and, secondly, by means of the finest branches of the protoplasma processes which go to form the nerve fibre network of the gray substance.

Fig. 248.

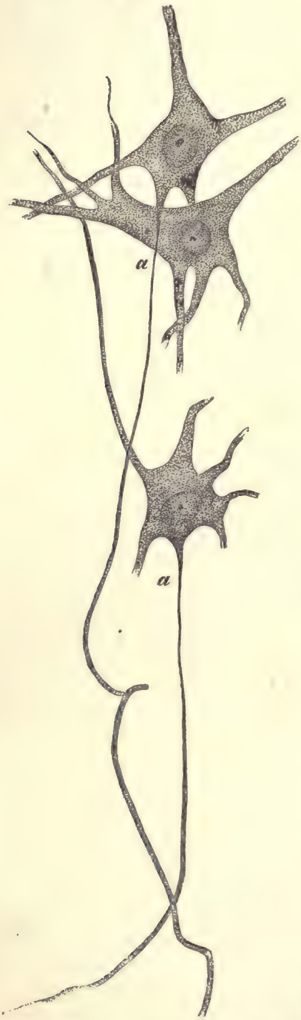

Fig. 248. Nerve cells from a longitudinal section of a Calf's spinal cord treated with ammoniacal carmine. *a a*, nerve processes proceeding horizontally forward. Magnified 150 diam.

The third question, that concerning the invariable presence of nerve processes on the ganglion cells of the gray matter, is an exceedingly difficult one to answer, because the nerve process is only exceptionally visible in sections; and there is this objection to dilacerated preparations, that the slender portion which unites the nerve process with the cell may have been broken off in the manipulation. It was natural that Deiters should have applied his important discovery to all nerve cells in the spinal cord; the more so because he

had observed nerve processes on small as well as on large ganglion cells. Deiters says nothing as to the possible existence of cells devoid of nerve processes. I believe that I can partially answer the question, since having, with this object in view, made a special study of a particular group of nerve cells, composed of medium-sized cells, and lying near the middle of the spinal cord, about equi-distant from the points of entrance of the anterior and posterior roots. It is that cell-group which has already been described, limited to the dorsal region of the spinal cord, and which is known by the name of Clarke's column. As these cell-groups are difficult to find in the fresh spinal cord, I made use of portions of that organ which had been hardened in a solution of bichromate of ammonia; and hardened only just enough to allow the cutting of transverse sections. These sections were stained with ammoniacal carmine and then soaked in glycerine, in which they soon attained a degree of softness which permitted the making of preparations by dilaceration with needles. On sections prepared in this manner, it was very easy with a low power to see nerve processes, isolated for considerable distances, attached to the large nerve cells of the anterior horns, and also to the small ones of the median portions of the gray matter. But it never happened to me to observe a nerve process upon any cell belonging to Clarke's columns. Inasmuch as I possess a certain expertness in observing nerve processes, and as these are not easily overlooked even when torn off, I believe that I am in a position to assert with tolerable positiveness that all ganglion cells do not possess nerve processes. Consequently we must recognize in the spinal cord two morphologically different kinds of cells; one which is in direct communication with the fibres of the anterior roots and with the nerve fibre network of the gray matter, the other united only with the latter.

It would seem very reasonable to attribute different physiological properties to nerve cells so different anatomically, and yet I am perfectly aware that it is a very uncertain and hazardous matter to draw physiological conclusions from purely morphological data. Nor do the attempts of this sort already made on the spinal cord invite imitation. Jacubowitzsch,* as is well known, transferred Bell's law, which had been applied with more or less success to the columns of the cord, to the gray matter, calling the large cells of the anterior horns motor, the small cells of the posterior horns sensitive elements. And yet even half-educated physicians are aware that in the portion of the spinal cord which constitutes the medulla oblongata, neither the conditions of willed motion nor those of sensibility are known. There may exist anatomical elements in the spinal cord, which neither produce the impulse of motion nor through which sensation is perceived. Of the various forms of cerebral activity appertaining to the cerebro-spinal axis, there are only two existing in the spinal cord, viz., the reflecto-motor and the automatic. The temptation is consequently great to connect these two varieties of central activity with the two different sorts of cells in the spinal cord, and to consider as reflecto-motor the nervous cells possessing nerve-processes, as automatic those exhibiting only protoplasma-processes. This hypothesis is further supported by the fact, now rendered more than probable, that the former of these cells are in direct union with the muscles, by means of the nerve processes through the anterior roots; and by the observations of Max Schultze, according to whom the fibrillæ constituting the nerve processes as well as the protoplasma processes of nerve-cells, do not originate in them,

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* *Mittheilungen über den feineren Bau von Gehirn und Mark.* Breslau. 1857.

but traverse them, a view which in a certain degree renders intelligible, in a morphological way, at least, the absolute non-occurrence of transfer of irritation from one nerve fibre to another.

Having now learned to recognize the anatomical elements as constituting the gray matter, we are now prepared to undertake a closer study of its several parts.

The median portion of the gray matter, the so-called gray commissure, is made up of several histologically different portions. Not exactly in the middle, but a little forward of it, is the central canal (fig. 249, *c*), lined by cylindrical epithelium, the substratum of which is composed of connective tissue, quite devoid of nerve fibres (fig. 249, *e*). In front of this, immediately behind the white commissure (fig. 249, *i*), the commissural fibres (fig. 249, *h*) belonging to the posterior commissure appear running from right to left, while just behind the central canal expands a delicate nerve fibre network (fig. 249, *f*), behind which appears the posterior commissure (fig. 249, *g*), which in the median line lies against the posterior longitudinal fissure, and laterally against the posterior columns (fig. 249, *b b*).

Fig. 249.

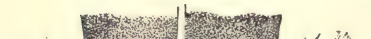


Fig. 249. Central portion of a transverse section of the lower cervical region of a six months Child's spinal cord, treated with chloride of gold and potassium. Magnified 50 diam. *aa*, anterior columns; *bb*, posterior columns; *c*, central canal; *d*, line representing the epithelium of the central canal; *e*, connective tissue lying immediately round about the central canal; *f*, nerve fibre network surrounding the central canal; *g*, posterior transverse fibres of the gray commissure; *h*, anterior transverse fibres of the gray commissure; *i*, decussation of the anterior white commissure.

The central canal is not of an uniform diameter throughout the cord, presenting in transverse section an ovaloid outline in the cervical region, a rounded one in the dorsal region, while in the lumbar region it has a more or less cordiform shape. It begins at the lower end of the fourth ventricle, and extends in Man, as determined by Stilling,* down into the *conus medullaris*, in which it approaches nearer and nearer to the posterior longitudinal fissure, and finally unites with it. This canal is filled, in young Adults and Children, with the cerebro-spinal fluid; but in Adults it is compressed, and, especially in the cervical region, obliterated; or, more properly speaking, choked up with the product of epithelial cell proliferation, which begins to show itself soon after puberty; at least I once found evidence of it in the cord of a Girl eighteen years of age. The innermost layer of the central canal is a tissue composed of cylindrical epithelial cells (fig. 250, *b*), which in Children exhibit vibratile cilia, which are lost in later years. In chromic preparations delicate thread-like processes may be seen, leaving the sharp extremities of the cells, and extending into the connec-

* *Neue Untersuchungen über den Bau des Rückemarks.* Cassel. 1857.

tive tissue. The space between these appendages is filled up with a very finely granular substance (fig. 250, *d*), which I take to be connective tissue devoid of elastic fibre network. In this substance, between the tapering ends of the epithelial cells there are a few nuclei surrounded by a small amount of protoplasma (fig. 250, *c*), which become more numerous with advancing age, and can serve no other purpose than to contribute to the development of new epithelial cells. Under this finely granular substance lies a network of fine fibres with exceedingly narrow meshes, in the midst of which cellular elements appear here and there (fig. 250, *a*). I look upon this structure as a form of connective tissue, which in this situation differs from that which is so abundantly represented in the gray matter as neuroglia only in this, that the fibres constituting the network, which have already been minutely described, and which are to be considered as elastic fibres, are much more numerous. This peculiarly constituted neuroglia, the so-called ependyma of the central canal, is bounded on either side and behind by a network of fine nerve fibres, which often appears with extraordinary beauty in gold preparations, and in which a few small cells are here and there embedded. The meshes of this nervous network are wider than those of other portions of the gray matter, which fact indicates a greater abundance of connective tissue in this region. Behind this nerve fibre network, as well as immediately in front of the ependyma of the central canal, there pass over horizontally in the median plane bundles of delicate nerve fibres, which unite both halves of the spinal cord, and which are denominated the anterior and posterior commissural fibres of the gray substance. The posterior, which are in immediate contact with the connective tissue of the posterior septum of the pia mater, are more numerous than the anterior; both may, however, be seen with the greatest distinctness in gold preparations. The results of experimental physiology (Brown-Séquard) render it probable that these delicate horizonally disposed fibres of the posterior gray commissure are connected with sensitive brain-tracts, while the larger decussating fibres of the anterior white commissure ascend to such regions in the brain as give impulse to willed movements.

Fig. 250.

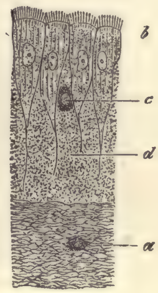


Fig. 250. Wall of the Human central canal. Magnified 300 diam. *a*, fibrillated connective tissue, with a cellular element; *b*, ciliated cylindrical epithelial cells with thread-like appendages; *c*, ciliated cells in way of development; *d*, finely granular substances between the thread-like processes of the ciliated cells.

Both halves of the gray matter of the spinal cord exhibit the well-known anterior and posterior horns, which are not, however, separated by any distinct limit. Description becomes easier if we admit the existence of an intermediate region lying behind the anterior and in front of the posterior horns. The anterior horns are distinguished by the presence of groups of large nerve cells, three of which may be distinctly recognized in the cervical and lumbar portions of the cord. The largest of these cell-groups, that which extends farthest backward, is the lateral (fig. 240, *n*), the smallest the internal (fig. 240, *p*), and a little larger than this the anterior (fig. 240, *o*), which lies externally in front of the lateral. In the anterior horns of the dorsal region, in which the number of nerve cells is notably smaller, these groups are more or less completely blended. Besides, there are other nerve

cells of various size which do not belong to definite groups. The anterior horns are, moreover, traversed by nerve fibres, singly or in bundles, some of which form part of the anterior roots uniting with the nerve processes of the cells; others, originating from the nerve fibre network, which enter into the anterior column of the opposite side, as well as in the lateral column of the same side. The nerve fibre network is closely embedded in connective tissue, with the exception of that portion lying in the immediate vicinage of nerve cells, which, both in gold and carmine preparations deprived of water and mounted in Canada balsam, always presents a moderately wide transparent space, which may possibly represent unstained, and consequently invisible connective tissue.

Fig. 251.

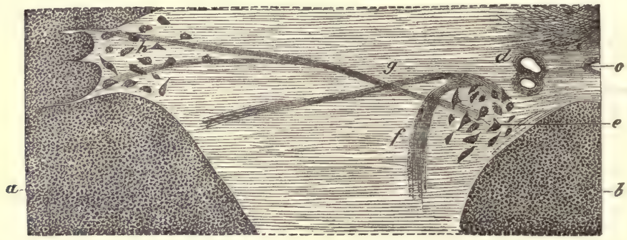


Fig. 251. Intermediate portion of a transverse section of a Child's spinal cord in the dorsal region; gold preparation. Magnified 50 diam. *a*, lateral column; *b*, posterior column; *c*, half of the central canal; *d*, cross-sections of blood-vessels; *e*, Clarke's column; *f*, fibres running backward from Clarke's column; *g*, point of intersection of outwardly proceeding fasciculus; *h*, lateral group of large and small nerve cells.

The intermediate portion of both halves of the spinal cord presents a noteworthy cell-group only in the dorsal region. It is that which we have so often mentioned under the name of Clarke's column, which lies a little to one side of and behind the posterior gray commissure. These columns attain their greatest development in the middle of the dorsal portion of the cord; that is to say, they there contain the greatest number of medium-sized cells. Toward the cervical and lumbar regions these cells become fewer and fewer, until, at the beginning of the cervical and lumbar enlargements, they have wholly disappeared. By means of gold preparations I have succeeded in discovering sharply-marked bundles of nerve fibres in close relation to this cell-group. Two bundles of fibres start together from the anterior limit of the group, one of which turning upon itself proceeds backward (fig. 251 *f*), while the other extends outward to the lateral column, crossing on its way thither still another bundle of fibres, which leaves Clarke's column and likewise ranges outward (fig. 251 *g*). If we do not, at every level in Clarke's column, find precisely the same arrangement of these fasciculi, yet throughout their whole extent the fasciculi which proceed backward and outward are invariably present. As regards the ultimate destination of these fasciculi, I have as yet made no conclusive observations: perhaps that which proceeds backward ultimately joins the posterior nerve roots. The remainder of the intermediate region histologically resembles those parts of the anterior horns which are without cell-groups, except that in the inner and posterior portions ascending nerve fibres appear extending as far as the gray commissure, where they traverse the lateral part of the posterior transverse fibres.

Externally, more especially in the cervical portion of the cord, the limit between the white and gray substance is not as sharply drawn as elsewhere, for the reason that the gray substance is traversed at various depths by separate bundles of fibres derived from the lateral columns; giving rise to the so-called reticulated formation.

The posterior horns are naturally divisible into two sharply-defined portions, an anterior (fig. 244 *c*), and a posterior; which last, owing to the peculiar translucent appearance it presents to the unaided eye, has long been known by the name of gelatinous substance of Rolando (fig. 244 *d*). This is the part of the gray substance which is poorest in nervous elements, and it is distinguished from other parts of this substance by its not possessing the delicate nerve fibre network. It is, however, very rich in connective tissue which presents certain peculiarities. Of the three forms under which connective tissue appears, viz., (1) a finely granular fundamental substance; (2) cellular elements, and (3) delicate fibrillæ, which I consider akin to elastic fibres; the last are very scanty, whereas the cellular elements under the form of nuclei, surrounded by a minute portion of protoplasma, appear in great numbers. This is the reason why in successful carmine preparations the gelatinous substance next to the epithelium of the central canal exhibits the most intense color. The nervous elements of the gelatinous substance are limited to small horizontal bundles of nerve fibres, derived partly from the posterior roots and partly from the posterior columns; these,

Fig. 252.

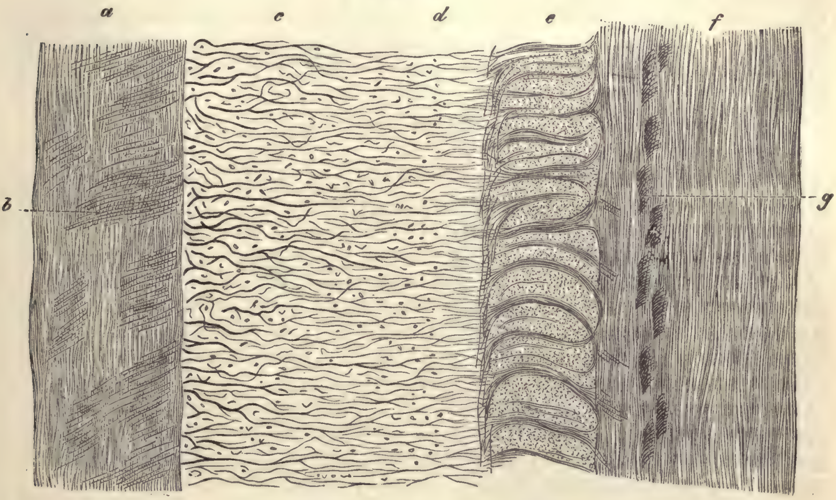


Fig. 252. Antero-posterior section through the lumbar region of the Human spinal cord treated with chloride of gold and potassium. Magnified 30 diam. *a*, anterior columns; *b*, anterior nerve roots piercing the anterior columns obliquely; *c*, anterior horn; *d*, posterior horn, with the vertically ascending bundles of nerve fibres lying in front of the substantia gelatinosa; *e*, gelatinous substance pierced by horizontal bundles of nerve fibres; *f*, posterior column; *g*, posterior nerve roots cut across in their course to one side.

however, only traverse this substance, the middle bundle in a pretty nearly straight line, the external in a curve, in order to reach the anterior portion of the posterior horns, that which contains a nerve fibre network (fig. 244 *d*).

Lastly, as regards the shape presented by the gelatinous substance in transverse sections, it exhibits an elongated oval outline in the cervical and dorsal regions, and appears more circular in the lumbar. The inner, and to a certain extent the posterior edges of the gelatinous substance, border on the posterior columns and the posterior nerve roots; externally and in part posteriorly, it is surrounded by a clear border of gray substance of the posterior horn, made up of a nerve fibre network in which there occur, here and there, large nerve cells; and immediately anterior to which are to be seen bundles of nerve fibres traversing the gray substance vertically (fig. 244 *h*, fig. 252 *d*).

The anterior division of the posterior horn is exceedingly rich in nerve-fibres, horizontally and vertically disposed; the former being here characterized by their frequent subdivision, and may be traced with tolerable facility as far as on a level with the central canal. The vertical fibres mostly ascend in a large bundle, above referred to, placed in front of the gelatinous substance (fig. 244 *h*). This fasciculus of vertical fibres is connected with the posterior columns, and in part with the posterior nerve roots by means of numerous horizontal and oblique nerve fibres which run backward through the gelatinous substance. In very successful gold preparations, however, fibres proceeding forward may be seen, which either leave this vertical bundle or join it. Besides these vertical fibres united in a bundle, others having a like direction appear, which, lying a little more inward and forward, encroach to a certain extent upon the intermediate part of the gray matter. The nerve cells of the posterior horns are of medium and smallest sizes, and are not, as are those of the anterior horns, united in groups, but lie scattered in that portion of the posterior horns which is made up of fine nerve fibre network, similar to that present in the anterior horns.

Course of Fibres in the Spinal Cord.

We are hardly prepared, with the means and methods of investigation at present at our command, to enter into a detailed description of the course of nerve fibres in the spinal cord; a description which would be a sure foundation for a physiology of that organ. However, the foregoing observations warrant at least the tracing of a sketch, which, as regards the direction pursued by the fibres which enter in with the anterior nerve roots, will have a pretty sure basis, while, contrarily, as regards the course of fibres which, passing through the posterior root, penetrate the cord, it will be to a certain extent fragmentary and uncertain.

After their entrance into the cord, the fibres of the anterior roots traverse the white substance obliquely, and take no part whatever in its formation, but proceed directly to the gray substance, where they enter into intimate union with the nerve cells of this region by means of the nerve-processes; which cells are consequently to be looked upon as the source of origin of the anterior root nerves in the spinal cord. The protoplasma processes of these cells constitute portions of the delicate nerve-fibre network of the gray substance, out of which broader nerve fibres are developed, which, leaving the gray substance to ascend toward the brain by way of the white substance, proceed in two directions. As a consequence of the continual entrance of new nerve fibres into the white substance, the latter must of necessity increase in size from below upward. As regards the course of the fibres leaving the gray substance of the anterior horns, two varieties are to be distinguished: an internal and an external. The internal set of fibres immediately enter the anterior white commissure, in which they

decussate with similar fibres coming from the other side, reaching the anterior column of the opposite half of the cord and ascending therein. The external fibres repair to the lateral column of the same side, proceeding upward in them, ultimately decussating in the medulla oblongata.

The fibres of the posterior roots proceed in a horizontal plane, from without toward the median line in the white substance of the cord, subdividing into two bundles. The lateral and smaller one preserves its horizontal course, and, dividing into smaller and smaller fasciculi, pierces the gelatinous substance in the manner above described, on its way to form a part of the fasciculus of vertical fibres lying immediately in front of the gelatinous substance, and in which some of the fibres ascend, others descend. These external fibres of the posterior roots do not, however, remain long in this vertical fasciculus, but bend forward in the horizontal plane, reaching that portion of the posterior horns consisting of nerve fibre network.

The internal larger fasciculus of the posterior root fibres lies against that portion of the posterior columns which adjoins the gelatinous substance internally and posteriorly, and, bending here, takes a vertical direction, ascending for a considerable distance in the posterior columns, and probably descending in them also. These fibres once again undergo a change of direction by which they resume their horizontal course, a part of them traversing the inner portion of the gelatinous substance, another entering into the inner border of the gray substance of the posterior horn. It is impossible to come to any positive conclusion relatively to the further course of the fibres of the posterior roots, because we have as yet no means of distinguishing these fibres from such as form the vertical bundle of the posterior horn, or such as, leaving the gray substance, ascend to the brain through the posterior columns. The numerous divisions which the fibres constituting the posterior roots undergo, immediately after their entrance into the cord, indicate that a part of them, at any rate, lose themselves in the nerve fibre network of the gray substance of the posterior horn. Besides, there are numerous fibres which proceed forward, and others which take an undulating course inward. The former may be accepted as part of the posterior roots, which farther forward enter into the formation of nerve fibre network; the latter become commissural fibres, which traverse the median line in front of and behind the central canal. In my opinion these fibres, forming part of the posterior commissure, are not to be looked upon as coming directly from the posterior roots, but rather as fibres which turn back in order to ascend toward the brain by way either of the vertical fibre fasciculus of the gray substance, or of the posterior columns. Should this view prove correct, and in its favor we have the occurrence of analogous dispositions in the anterior horns, the following may be assumed with regard to the course through the gray substance of fibres entering in with the posterior roots. *A portion of the nerves of the posterior roots, immediately after its entrance into that part of the gray substance containing nerve-fibre network, enters into the formation of this network; another portion extends in a bundle still further forward, and, while advancing, separates into more and more frequent subdivisions, which ultimately, in all likelihood, merge into the nerve-fibre network. This network, in which large and small nerve cells appear embedded as knots (Knotenpunkte), is continuous with the network of the anterior horns. From it are developed nerve fibres which cross the median line in front of and behind the central canal, then incline backward, some of them ascending to the brain in the vertical fibre fasciculus of the posterior horns, others in the posterior columns, between which latter there may exist decussations as yet undemonstrable.* This conception necessitates a total decussation in the cord of those fibres which enter it through the pos-

terior roots; although as regards those nerve fibres which, developed from the nerve-fibre network, return backward without crossing the median line to enter the posterior columns, purely anatomical means will not allow us positively to decide whether their decussation is partial or complete; although pathological observations as well as the experimental results of that most competent investigator in this department, Brown-Séquard, indicate a complete crossing over.

In bringing this article to a close I may be allowed to give prominence to two points.

1st. In the distribution of the nerve fibres entering in through the posterior roots, the gray substance plays a much more important part than in that of those which reach the spinal cord through the anterior roots.

2d. The difference, which is to be considered as a morphological one, between the fibres of the anterior and those of the posterior roots, consists in this; that the former, by means of the nerve processes, arise directly from nerve cells, whereas the latter are united with nerve cells only indirectly, by means of the protoplasma processes, through the nerve-fibre network.

Translator's Note on the Mode of Preparation of the Nervous Centres for Microscopical Examination.

During the past three years I have given as much time as I could spare from the duties of private practice and from those connected with dispensaries, etc. to the investigation of the normal structure of the nervous system, and to the study of such morbid conditions of that system as have come under my notice. At the first I employed the method of preparation made public in 1859 by J. Lockhart Clarke, of London. This method consists in hardening the spinal cord and brain, cut into pieces or blocks of an inch or more in various dimensions, in solutions of chromic acid, one part to three hundred for the cord, and one part to four or five hundred for the brain. After a lapse of three or five weeks (the solution to be renewed once every week or ten days), the segments of nervous tissue are ready for the next step in the method, viz., the cutting of thin sections from them by means of a razor. These sections are to be stained in an ammoniacal solution of carmine, then soaked in common alcohol to extract the water, transferred to absolute alcohol to complete the anhydration, and, lastly, floated upon oil of turpentine until they become transparent and sink. These stained and transparent sections may be made into permanent preparations by mounting them in Canada balsam upon a glass slide. By means of this method very good specimens are obtained.

During the last eighteen months I have obtained better results by means of a modification of this method, the improvement consisting mainly in the more perfect demonstration of nerve fibres. I can most clearly describe this modified Clarke's method by considering separately the four principal stages in which it consists—hardening of the nervous centres, cutting of sections, staining the sections, mounting them as permanent preparations.

I. (*a*) To harden the spinal cord, I remove its serous coat only, and cut it into segments measuring about 2 c. in length. This cutting should be done with a very sharp razor, perpendicularly to the long axis of the organ, and in pathological cases the surfaces of these sections should be studied and their appearance noted before any reagent has modified the nervous substance. I then fasten these segments in their natural order upon one or two threads, suspending these threads in a jar containing a quart at least of a solution of bichromate of potassa of the standard strength (gr. xv. to ℥ i).

At the end of a week or ten days the specimen is transferred to a solution of chromic acid, strength one part to five hundred. This chromic acid solution should be changed every week or oftener. At the end of three or five weeks from date of immersion in chromic acid, the hardened cord should be placed in strong alcohol, and after three days the second step in the method may be proceeded with. The cord may be left in alcohol almost indefinitely without undergoing any destructive changes. (*b*) To harden the brain, I leave the organ, having opened it by one or more sections in such a way as to expose the ventricles and central ganglia, in the standard solution of bichromate of potassa or in Müller's fluid* for one or two weeks, or even longer. From such portions of the brain as it is desired to study, pieces are cut by means of a razor in the shape of blocks measuring from 2 to 4 c. in the various dimensions, and these blocks placed in strong alcohol. After the lapse of a week or ten days, sections may be cut from these blocks with facility. [Occasionally, previous to placing them in alcohol, I soak the blocks for a week in a solution of chromic acid of the strength of one part to six or eight hundred.]

II. Cutting sections. (*a*) Sections from the spinal cord I always make by the help of a simple section-machine devised by my friend Dr. Louis Ranvier, of Paris. It consists of a brass tube a little larger than the spinal cord, terminating at one end in a circumferential platform lying exactly at right angles with the long axis of the tube. The other end of the tube is closed by a cap perforated to allow of the working of a sort of piston up and down in the tube by means of a very fine screw-thread cut in the exact centre of the cap, and upon the piston. The specimen being placed in the tube resting upon that end of the piston which is inside the tube, revolutions of the piston cause an elevation of the specimen up to the platform end of the tube. A razor ground flat on one side is used for cutting slices from the specimen as it is raised beyond the level of the platform, upon which the flat side of the razor is made to play with pressure. The advantages of such a machine are, that it insures the making of thin and even sections, in great number; that it facilitates the cutting of sections at right angles to the axis of the spinal cord; and, lastly, that it renders possible the economizing and utilizing of a very small specimen. Before placing the segments in the section machine, I mark them in such a way that when the sections are mounted I am enabled to distinguish the right from the left halves. In an unmarked section of the spinal cord it is impossible, because of the absolute similarity of the two section-surfaces, so to distinguish the sides; and I have been surprised to observe no hint given by writers upon the subject. I make a shallow longitudinal incision in the middle of the right lateral column, going just fairly through the peripheral layer of reticulum. In sections cut from such a marked segment of cord, each right half appears with a slight nick or break in the outer edge of the lateral column. Having so marked the segment, I place it in the machine, and fasten it in the tube by means of an embedding substance; either elder pith of such a size as to allow of perforation and of the introduction of the segment without violence, or a melted mixture of white wax and olive oil, two parts of the former to one of the latter. The advantages of the pith (which is difficult to procure of the required diameter) are, that it swells when it has imbibed water or alcohol, thus compressing the enclosed specimen firmly yet safely; and that its texture is so fine that the razor-edge is less injured by passing through it than

* Müller's fluid may be made according to the following formula: bichromate of potassa 2 parts, sulphate of soda 1 part, water 100 parts, by weight.

through any other embedding substance. In pouring the melted oil and wax around the specimen (in a paper mould or in the tube of the machine), care should be taken that its temperature be not too high. When the specimen is secured in the pith, or when the wax about it has thoroughly hardened, it may be introduced into the section-machine, and pushed up by means of the piston until its extremity rises just above the level of the platform. The platform and specimen then being well wet with alcohol, and the razor likewise, a preliminary cut is made to expose a fresh and smooth surface. A partial revolution of the piston (from $\frac{1}{8}$ to $\frac{1}{4}$ circle) elevates the specimen enough to allow of a fine section, fit for further manipulation, to be cut. In cutting the machine is to be held firmly in the left hand, in such a way that the platform shall be horizontal (to retain the alcohol which is upon it), and the razor drawn across it by the operator in a direction toward his body and toward his right, an oblique movement to the right and rear. The cut being finished, the section adheres to the blade of the razor, and is to be removed by agitating the razor in a shallow dish of alcohol. A point that will bear insisting upon is, that during the operation the platform and razor should be thoroughly wet, even flooded, with alcohol. I treat the medulla oblongata, the pons varolii, and blocks of brain in precisely the same manner, using a larger section machine. (*b*) Sections from the hardened blocks of brain (cerebrum) may be cut without a machine, the specimen being held between the thumb and forefinger of the left hand, its surface well moistened, and the razor drawn through it in the manner above described. A constant practice in hand-cutting is however requisite to secure the making of good sections, for sections of this tissue, to be of any value, must be most delicate and even.

III. The sections removed from cord or brain in the way above detailed, and floated off from the razor in alcohol, are now to be stained. I transfer the sections from the alcohol to water, in which I allow them to remain a few moments, until the water has removed the alcohol from them. (This transfer and all handling of the sections I achieve by means of steel spoons which I have had constructed, and which may serve for the handling of sections of other tissues. These spoons are modified knives for operating about the palate, consisting of a long handle with a rounded blade of polished steel, having its flat side turned up at right angles to the handle. The section may be picked up on this flat surface and carried to another fluid, without risk of laceration or folding. I have had two sizes made; one for the cord, measuring 8 mm. across the blade, the other for the medulla oblongata and brain, 18 mm. in diameter; and a still wider one would be useful.) For staining I use a modified Beale's solution of carmine, made according to the following formula: carmine, ten grains; aq. ammonia, a few drops; alcohol, half an ounce; glycerine and water, of each one ounce; to be mixed and filtered with care. Of this carmine solution I pour a quantity into a watch-glass, or other suitable vessel, and add an equal volume of water. In this dilute solution I place the sections, preventing their contact with the glass by means of a small piece of blotting paper sunk in the solution. The watch-glass and contents are now set aside and covered, so as to exclude dust and retard evaporation. After two, three, or even six days, the staining is complete, and I wash the sections in water. This is an exaggeration of the method of slow staining, accidentally discovered by Gerlach, and by it I have obtained superb staining of the fibres of the anterior roots as they radiate in the anterior horns. An objection to the plan is that much time is needed; an objection which I can best answer by asserting that any one who expects to study the normal and patho-

logical histology of the nervous system without the sacrifice of much time will be severely disappointed.

IV. The stained sections must now be prepared for examination—they are to be made transparent and "mounted." The sections are to be transferred from the water in which the superabundant carmine solution and particles have been washed off, into strong alcohol. From this, after half an hour or longer, they must be removed to absolute alcohol, which takes out the last trace of water contained in the sections. I sometimes use turpentine (Clarke's original process) to finish, or, more often, light-colored oil of cloves; the advantage of the latter lying in its more pleasant odor. When the sections are placed in the oil of cloves, after removal from the absolute alcohol, they float, and gradually imbibe the oil. In a few moments the section becomes at the same time saturated with oil, quite transparent, and sinks.

The "mounting" is done in this wise. The section to be mounted is raised out of the oil of cloves by means of a spoon, the excess of oil allowed to drip off, and the section gently pushed from the spoon upon the centre of a glass slide. At this stage it is important that no moisture strike the section (it should not be *breathed upon*), or else it becomes opaque once more. A large drop of a solution of Canada balsam in chloroform (enough chloroform to make the balsam perfectly fluid) is then placed on the section, and a thin covering-glass dropped over it in such a way as to exclude all air-bubbles. Such a preparation does not become solid for weeks, or even months, so that if it is to be transported, or much handled, a ring of some cement should be added, to prevent sliding of the thin glass.

E. C. SEGUIN.

CHAPTER XXXII.

THE BRAIN OF MAMMALS.

By THEODOR MEYNERT,

IN VIENNA, AUSTRIA.

General View of the Construction of the Brain.

The elementary forms concerned in the construction of the brain present no great variety in kind, while on the other hand the greatest possible variety is to be observed in the manner in which they are grouped. As, therefore, the significance of the elements can be determined only by their position and relations, a purely histological exposition could contribute but little to an understanding of the organ under consideration. The minute structural details of the grouping also must unavoidably be kept in mind, as well as the bearing of all matters of minute-anatomical interest upon the gross-anatomical relations of the larger masses. Now, although these considerations call for the treatment, within the following pages, of facts not strictly histological, yet the requirements of a text-book demand a brevity which renders an exhaustive treatment of the subject impossible. Those, however, who wish to study the matter more closely will be referred to the primary sources of information.

While now this increase of space allotted to morphological considerations admits of a more satisfactory treatment of our subject, the reader will be materially helped to a clear understanding of it, if he will allow three fundamental ideas, which underlie the plan of construction of the brain, to accompany and light him through its intricate ways.

1. The recognition of *sensibility* as a functional attribute of the nerve cell. Strictly subject to the limitation that this sensibility becomes actual sensation only under favorable conditions, it must be conceded to be a universal attribute of the central nervous cell element.

The results attained by physiological investigations do not justify us as yet in locating the process of sensation exclusively in any special section of the central nervous system, as, for instance, in the cerebral lobes. Such being the case, the important fact must also not be forgotten, that at the lowest extremity of the Vertebral series is found a creature (Lancelette)* of which the central nervous system consists of the gray spinal cord alone, but to which we are not justified in denying a conscious animal existence.

On the other hand, we must not attribute to the nerve cell any other inherent property, as for instance the ability to originate motory impulses. Of all the tissues of the body, that of the muscles alone is possessed of motor properties, and if any condition of excitation induced in the nerve cell (which may indeed be identical with the process called sensation) finds

* Lanzetfischchen.—Translator's Note.

communicating paths, acting through which it can call into play this functional activity of the muscles, the part taken by the central system in the production of such motions may be satisfactorily assumed to consist merely in supplying the above-mentioned mechanism for the conduction of the exciting impulse, whether the final motion in question follow the excitation which gave rise to the sensation, mediately or immediately in point of time, and whether the conducting path simply pass through the shortest diameter of the spinal cord, or through an immeasurable chain of interruptions along the curved conductor-like nerve tracts of the cerebral lobes.

2. The second point to be held in mind is BELL'S LAW—so extended as to include the expression of the fact that the centripetally and centrifugally conducting nerve tracts are prolonged upwards until, undisturbed in their course by the reduplications and dismemberments to which the white substance is subjected in passing through the gray nodal masses, they penetrate to the most distant centres of the cerebral organism, or, more strictly speaking, find there their origin.

3. Thirdly, is the all-pervading sway of *the law of isolated conduction* to be remembered, which finds its morphological expression in the fibrillation of the white substance. But also in the gray masses, where the formation of anastomoses undoubtedly paves the way for cross-conduction, the law of isolated conduction still obtains, though not unconditionally. Here also it finds its morphological expression in the fact that the nerve cells lie with the long axis stretched in the direction of the fibres with which they stand in connection. Certain facts force upon us the assumption that the resistance to conduction is less in the direction of this axis than in the gray fibrous network of the ganglion substance, and it is to this circumstance that the preservation of the isolation is due.

A valuable *general view of the principal features of the structure of the brain* is to be had from transparent sections of the brains of *small Mammals*, where, under a low magnifying power, the general course of the fibres as well as the relative disposition of the masses is to be recognized.

The nerve cells of the brain occur in gray masses, which may be divided into four categories:—

1. The *uppermost* mass of gray matter, from which the entire medullary substance of the brain takes its rise, is the *superficial gray substance* of the cerebral lobes—the *cortex cerebri*.

2. The second division of gray substance consists of the collections of gray matter found in the cerebrum, which, since the time of *Gall*, have been designated as the ganglia.

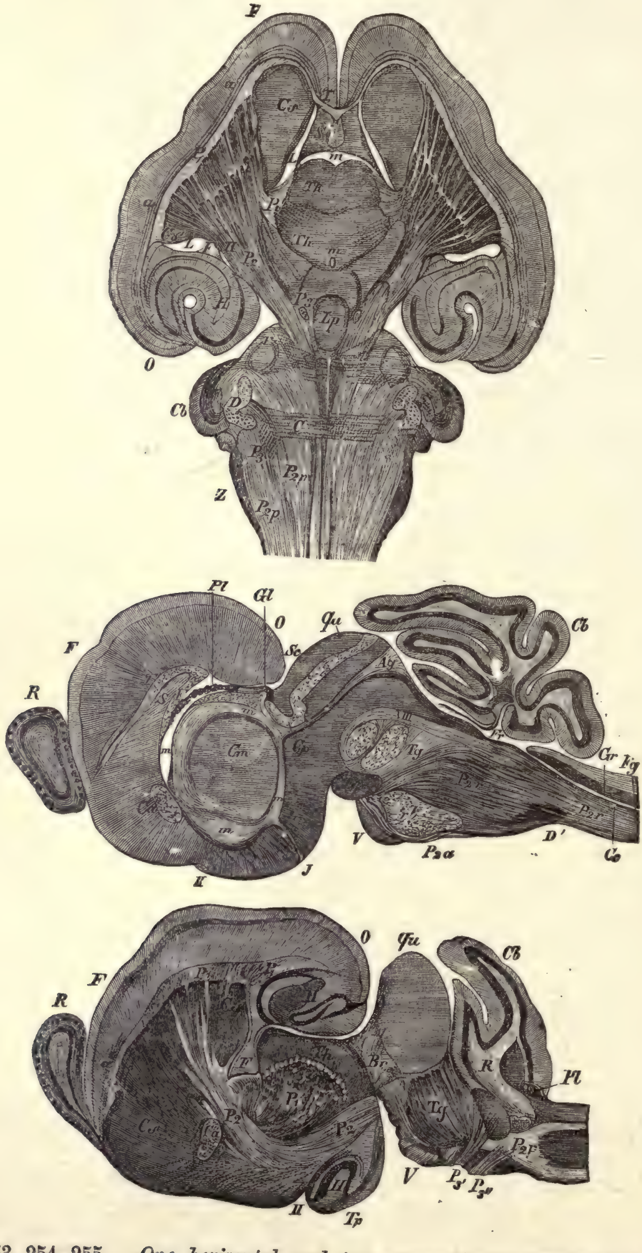
3. The tubular gray matter, the permanent expression of the primitive, genetic form of the brain, which, under the name of the *central tubular gray matter*, invests the inner surface of the central system, from the tuber cinereum to the conus medullaris of the spinal cord.

4. The *gray substance of the cerebellum*, which occurs partly in layers and partly as scattered cell-formations, and includes on the one hand both the superficial and the deep collections of gray matter belonging to the cerebellum, and on the other hand the gray substance formed within those segments of the caudex cerebri (Grosshirnstamm) which are traversed by the medullary substance of the cerebellum.

In order to get an idea of the scheme of construction of the brain, the most appropriate starting-point seems to be the assumption that the phenomena of consciousness are the expression of the functional activity of the cerebral lobes. Among other arguments in favor of this assumption is the consideration that the confluence of all the conducting tracts in this organ,

which is a morphological unit, finds an exact parallel in the confluence and union of all the processes of perception in consciousness.

Figs. 253, 254, 255.



Figs. 253, 254, 255. *One horizontal and two perpendicular longitudinal sections from the brain of Vespertilio pipistrella, intended to expose the principal features of the cerebral structure.*

Common designation—*F*, frontal extremity; *O*, occipital extremity; *Tp*, temporal portion of the cerebrum, or forebrain (prosencephalon); *R*, lobus olfactorius; *S*, septum lucidum; *H*, gyrus hypocampi, with *f*, the fornix; *T*, corpus callosum; *aa*, fibræ propriæ of the cortex (fibres belonging to the association-system); *L*, anterior and posterior horn of the lateral ventricle; *Cs*—*Cs*, ganglia of the forebrain (corpus striatum and nucleus lentiformis); *Th*, ganglion substance of the interbrain (diencephalon) [thalamus opticus]; P_1, superior member of the projection-system for the ganglia of the forebrain; P_1', superior member of the projection-system for the ganglia of the interbrain, to which *f*, the fornix, is also to be considered as belonging; *Qu*, the ganglion substance of the midbrain (corpus quadrigeminum)*; *Br*, superior member of the projection-system for the midbrain (processi ad corp. quad. Vierhügelarm); *Lp*, median basal surface of the midbrain (lamina perforata posterior); P_2, middle member of the projection-system from the ganglia of the forebrain (basis cruris cerebri, in fig. 255, cut off on account of its inclination toward the median line, in fig. 254, P_2a, continued through the pons varolii); *Tg*, the middle member of the projection-system coming from the ganglia of the midbrain and interbrain (tegmentum cruris cerebri); *VIII*, posterior longitudinal bundle of the tegmentum (Hintere-längsbündel der Haube); *Ca*, anterior commissure; *Cm*, anterior commissure (commissura mollis) of the thalami; *m*, central tubular gray matter of the interbrain (3d ventricle); *J*, infundibulum; *Ag*, central tubular gray matter of the midbrain surrounding the aquæductus Sylvii; *Gl*, pineal gland; *Cp*, posterior commissure; *Sc*, transverse fissure of cerebrum; *Pl*, choroid plexus; *Cb*, cerebellum; *R*, corpus restiforme; *V*, pons Varolii; P_2a, anterior pyramids (continuation of pedunc. cruris cer.); P_2r, continuation of tegmentum cruris cer. in the projection-system of the pons and oblongata; *Rb*, section through the transverse fib. of cerebellum; *Z*, section through the stratum zonale; *D*, superior olivary body; *C*, apparent commissure between sup. oliv. bodies; *D'*, inferior olivary body; *Fr*, central tubular gray matter occurring in the region of the hindbrain and afterbrain as 4th ventricle; *Gr*, central tubular gray matter in the region of the afterbrain and spinal cord around the central canal (*Cc*); *Fg*, funiculus gracilis; P_3, inferior member of the projection-system, represented in fig. 253, in the region of the midbrain by the nervus olfactorius, in the region of the afterbrain by the nervus facialis, in fig. 255; P_3', Quintus; P_3'', facialis; *II*, nervus opticus.

For this duty of embracing and binding together the conducting tracts, the cortex cerebri, in virtue of its form, that of a cap covering the surface of the rest of the brain (figs. 253, 254, and 255, *F*, *O*, *Tp*, *R*, *H*) seems well adapted. This form results from the manner of grouping of the numberless sensitive elements with which the cortex is peopled, *i. e.*, *the nerve cells.* The sensory nerve fibres constitute the feelers of these cells, the motory nerve fibres their tentacles, as it were. Whereas these fibres are obliged in great part to pass through the foramen magnum before they can reach the organs for which they are destined, they *converge* after the fashion of radii, tending always, within the caudex cerebri (Hirnstamm) and spinal cord, toward the central tubular gray matter. Having once traversed this central tubular gray matter they *diverge* again, and penetrate under the form of the peripheric nervous system to all parts of the body. Since now this organization of the body serves only to effect a contact between the perceptive hollow globe of the cortex cerebri and the external world presented under the varied portraiture of the senses, its image being thus, as it were, projected upon the cortex, the important section of the nervous system under consideration may be called the *projection-system*, the cortex cerebri being regarded as the *projection-plane*, and the outer world as the projected object (P_1, P_2, P_3).

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* In accordance with the custom of the author, although it be contrary to ordinary English usage, the Latin equivalent of the German *Vierhügel* is written corpus quadrigeminum instead of corpora quadrigemina. The superior pair of ganglia (obere Zweihügel) is rendered in similar manner corpus bigeminum superius, the lower, corp. bigem. inferius. (TRANS.)

Since the movements of the different parts of the body give rise to certain kinds of sensation (muscular sensation, sense of motion), this gives to the brain a representation of part of the projected outer world.

The muscular system is moreover *projected* in another sense, to wit, through the agency of the central and peripheric tracts of the motor nerves, along which the cortex cerebri reflects toward the exterior the excitation which has been already transmitted to it through the nerves of sensation.

In fig. 253. P_1, P_2, P_3, are seen the successive members of this projection-system, which suffers repeated interruptions in the masses of gray matter. Its uppermost member (P_1, P_1' and Br) consists of a system of medullary fibres which spring from the cortex cerebri, generally in radiate lines, and which find their peripheral termination in the gray matter of the 2d category, viz., of the ganglia. From out the interrupting nodal masses of the ganglia springs the 2d member of the projection-system (P_2), the crus cerebri, which ends peripherally in the gray substance of the 3d category, the tubular gray substance. The 3d member of the projection-system consists of the nerves proper, which take their rise in the above-mentioned central tubular gray substance throughout its whole extent, from the seat of origin of the 3d pair of the cranial nerves, to those of the lowest sacral nerves of the spinal cord. They terminate peripherally, perhaps without exception, in certain microscopic structures which are treated of in various parts of this text-book.

The course of the *first member* of the *projection-system* falls within the limits of the *cerebral lobes*, whose territory it shares, as may be seen without difficulty, with two medullary formations, the *trabecular-system and the arch-systems.* (Bogensysteme, made up of fibres which connect different regions of the same hemisphere, and which derive their name from the character of the curves they describe. v. fol.—TRANS.)

While the projection-system establishes a communication between the cortical cells of the brain and the external world, a threefold communication is set up between the same cortical elements within the limits of the cerebral lobes, and thereby that part of the protoplasm of the primitive germinal cell, which by its division gave rise to the countless cells of the cortical substance, comes together again to form a morphological unit, to explain the formation of which, a process of secondary consolidation must be assumed to take place. The most striking argument in favor of the justice of this assumption is afforded by the fact of the consolidation of the fibres of the corpus callosum in the median line, which takes place during fœtal life after the fibres of either side have broken through the inner wall of their respective cerebral vesicles. The fibres of the corpus callosum (figs. 253 and 254, T) connect together exactly *symmetrical regions of the cortex* of the two *cerebral hemispheres.*

The various parts of the cortex of one and the same hemisphere may, of course, be united by way of the gray fibrous network formed by the anastomosing cell-processes; nevertheless, the strongest argument for the assumption that the law of isolated conduction even here holds good, is furnished by the fact that, besides this network of gray fibres (without any medullary sheaths), the different regions of the cortex are bound together by nerve fibres, those constituting the fibræ propriæ, fibræ arcuatæ (v. above), which (figs. 253 and 255 *a a*) form a layer made up of longer and shorter bundles by which the inner surface of the cortex is uninterruptedly invested. Since, corresponding to this anatomical connection between the different regions of the cortex, there must be a connection, in regard to function, between the various states of excitation of the respective regions, effected by way of these

systems of nerve fibres, we may give to them in virtue of their office, as well as of their distribution, the name of *association-systems*.

A fourth category of nerve fibres of the cerebral lobes serves to unite the cortex of the cerebrum with that of the cerebellum. These fibres become compacted together, and under the name of the proc. cerebel. ad corp. gem. (Bindearm) constitute a distinct formation, which lies exposed to view at the level of the pons Varolii, but which, owing to the indirectness of its course from the one cortex to the other, as well as to its intimate and prolonged connection with the projection-system of the cerebrum, cannot be so described in this comprehensive sketch as to enable the reader to form a distinct conception of its relations.

The masses of gray matter situated below the cerebral lobes (with the exception of the central tubular gray matter as regards the 2d point) constitute

1. *Nodal masses* belonging to the *projection-system* designed to *interrupt* the course of the nerve-fibres of the same (Unterbrechungsmassen des Projections-system), and

2. Portions where the projection-system is reduced in size (Reductionsgebiete für dessen Umfang), for although its first member is of considerable size when, chiefly in the form of the corona radiata, it enters the various ganglia of the cerebrum, it is gradually reduced to the inconsiderable dimensions of the spinal cord (2d member of the projection-system).

This reduction of the projection-system relates not only to the *total number of fibres*, but also to the number of the separate *groups of fibres* which may be distinguished in the projection-system.

The first member of the projection-system divides, at the moment of its entrance into the various ganglia, into as many parts as there are nuclei of gray matter among the latter. Of such separable divisions may be distinguished, in figs. 253–255, the corpus striatum and the nucleus lentiformis with the groups of rays entering them (Cs and P_1); the thalamus opticus (Th), and corpus quadrigeminum (Qu) with their entering rays (P_1' and Br); and further a bundle of fibres whose course differs in character from that of the rest, the fornix (f), a division of the projection-system which connects a certain part of the cortex cerebri with the anterior tubercle (tuberc. anterius, vorderer Höcker) of the thalamus opt. The second member, however, of the projection-system, the crus cerebri (Hirnschenkel), appears, after leaving the ganglionic masses, so far simplified that only a twofold arrangement is to be distinguished, formed by the anterior and posterior division of the caudex cerebri, the basis cruris cerebri (Hirnschenkelfuss) (figs. 253, and 255 P_2), and the tegmentum cruris cerebri (Hirnschenkelhaube) (figs. 254, 255, Tg), which are prolonged as the anterior and posterior division of the pons and oblongata, and pass finally into the medullary investment of the spinal cord, a formation morphologically homogeneous.

This division of the projection-system into members, this (momentary) interruption of the course of its fibres by masses of gray matter, does not serve simply to effect a mutual exchange of excitations between different groups of ganglion-cells, placed one above the other, somewhat as buckets are passed up and down a ladder from hand to hand. The morphological significance of the interruptions depends rather (often demonstrably) on the fact that the cells thus introduced in the course of the nerve fibres, without breaking the direct, though jointed line of communication intended also for centripetal or centrifugal conduction, serve also to establish, by virtue of their deflecting power, a communication between the periphery and centres not situated on the direct path of the projection-system.

An example of such a deflection is furnished by the nervous tract, which has been proved by countless pathologico-anatomical observations to conduct centrifugally, and which leads from the cortex cerebri through the corpus striatum, nucleus lenticularis, basis cruris cerebri, pons and anterior pyramids of the medulla oblongata, to the roots of the anterior spinal nerves (figs. 253 and 255 P_1, Cs, P_2; fig. 254 P_2a). The great size of this tract before its entrance into the pons (while still basis cruris, Fuss des Hirnschenkels) becomes reduced to the insignificant dimensions of the anterior pyramids of the medulla, by the loss of a considerable group of fibres which branches off into the *cerebellum* through the processus cerebelli ad pontem (Brückenarme) and thus forsakes the projection-system. The fibres of the corona radiata which pass as a homogeneous formation from the cortex cerebri into, e. g., the nucleus lentiformis, encounter within this ganglion (in accordance with the above proposition) cells from out of which, although an immediate reduction of the number of fibrous elements takes place, nerve tracts spring, one of which is prolonged into the spinal cord, the other passes off into the cerebellum.

The division into two tracts (basis and tegmentum) which characterizes the simplified organization of the projection-system in the crus cerebri, allows of a natural division of the ganglia, which originate these tracts, into the ganglia of the *basis* and ganglia of the *tegmentum* cruris cerebri (Fuss u. Haube des Hirnschenkels). Among the former, the most important are the *nucleus caudatus* and *nucleus lentiformis*, among the latter the *thalamus opt.*, the *corpus quadrigeminum*, and the *corpus geniculatum internum*. Comparison of the basis and its ganglia with the tegmentum and its ganglia (in different animals) demonstrates that a significant independence of each other rules their development, a fact of fundamental importance as regards the variations in form of the Mammalian brain. It is the basis alone (with the parts belonging to it) which expands and contracts in size according as the cerebral lobes show a higher or a lower degree of development, which explains the fact that, of all animals, Man possesses the most fully developed nucleus lentiformis and basis cruris cerebri. The tegmentum with its ganglia, and especially the corpus quadrigeminum and corpus geniculatum internum, show their highest development, on the other hand, when that of the cerebral lobes is at its minimum. Hence the meagre development of the basis (figs. 253, 254, 255, P_2, P_2a) compared with that of the tegmentum (Tg, P_2r) in the brain of the Bat, where the cerebral lobes are so poorly represented. The important pathological fact that destruction of the ganglia attached to the basis causes complete hemiplegia, and the equally significant observation made by experimental physiology, that animals which have been deprived of every part of the brain except the ganglia of the tegmentum, are still capable of executing, in response to excitation from without, every variety of movement with perfect technical nicety, force upon us the conclusion that all parts of the body are represented in two-fold projection within the brain, viz., through the agency of the basis, and through that of the tegmentum cruris cerebri, while at the same time they are brought only by the basis into the relation of vital dependence in which they stand to the cerebral lobes.

The gray matter of the 3d category was excluded above from the gray masses designated as agents for effecting a reduction in volume of the fibrous mass of the projection-system; it seems, on the contrary, to effect a considerable increase in the same, as may be seen in the fact, now universally acknowledged, that the aggregate number of fibres in the roots of the spinal nerves considerably exceeds the number of fibres in the columns of the spinal cord.

This gray matter (fig. 254) appears first in the region of the interbrain (Zwischenhirn) as the lining of the third ventricle (m), which is made into a cylindrical-shaped cavity by the commissura mollis, and passes over into the lumen of the trichter (I).* Within the limits of the midbrain (region of the corp. quadrig.) it surrounds the aqueduct of Sylvius (Ag), within those of the hindbrain it expands to form the floor of the fourth ventricle (fossa rhomboidea, Fr), and throughout the lower half of the oblongata and the whole of the spinal cord (Gr) it surrounds the central canal (Cc). As of the spinal nerves, so also it is true of the cerebral nerves, which in figs. 253, 255, stand as the representative of the third member of the projection-system (P_3), that at their exit from the tubular gray matter, where they take their rise, they contain a number of fibres greater than that of those by which they are represented in the crus cerebri. From a superficial glance at fig. 253 it would appear that the process of reduction in volume of the projection-system gives place suddenly to a process of augmentation of the same in the region of the pons and upper half of the oblongata, since the circumference of a section made in this region exceeds that of the crus cerebri. This augmentation in volume is, however, to be explained in great part by the fact that within the region in question, through the agency of gray matter, to whose presence the increase in bulk is essentially due, the fibres belonging to the medullary substance of the cerebellum, which up to this point have been mixed in with the elements of the projection-system, branch off to enter the cerebellum, intertwining, as they go, with the fibres of the projection-system, which continue their own further course. The rapid diminution in size of the oblongata, which follows the completion of the above process, accompanies the transition from the cerebral organization to the organization of the spinal cord. Thus we see that the description of the construction of the brain naturally divides itself as follows:—

1. *The cerebral lobes.* 2. *The basis cruris cerebri, together with its ganglia.* 3. *The tegmentum cruris cerebri with its ganglia.* 4. *The region occupied by the interlacement of the processus cerebelli ad pontem (Brückenarme) with the projection-system.* 5. *The cerebellum.* 6. *The region occupied by the transition from medulla to spinal cord.*

1. The Cerebral Lobes.

Of 1,400 grammes—the weight of the entire Human brain—that of the cerebral lobes constitutes 1,100 grammes. The reason for their preponderance in size is perhaps to be found in the fact that, being the essential seat of memory, they contain at one and the same moment one portion of the exciting influences which act during the whole period of existence, whereas the other parts of the cerebrum are obliged to find room for the conditions of excitation of the moment only.

The gray matter of the first category, the cortex cerebri, invests the medullary substance of the cerebral lobes, and gives to the latter their external form. The cortex cerebri presents, in certain parts, peculiarities of structure which make it important to bear in mind certain points connected with its gross anatomy, in order that its textural peculiarities may be properly localized.

Genetically, the cerebral lobes make their appearance as two lens-shaped hollow excrescences on the sides of the anterior cerebral vesicle. The entire

* Funnel.

surface of the same develops into cortical substance. The external surface of the lens is of a shield-like convexity; the inner surface facing the basement (whence the lens-shaped excrescence sprang) must perforce have an annular form, and the lumen of the ring must be the communicating opening between the cavity of the anterior cerebral vesicle (1tes Hirnbläschen) and that of the hemispheric vesicle (Hemisphärenbläschen). The fibres of the corpus callosum, breaking through the inner wall of this ring, cut off a portion of its upper periphery, thus forming the septum pellucidum. For the rest, the ring-like surface of the hemisphere divides into an anterior, smaller, and a posterior, larger, segment, or (if we will) into two half rings. The *posterior half ring* becomes the *gyrus fornicatus*, the convolution which encircles the corpus callosum; the *anterior*, drawn out into the form of an angle, its opening looking backward, becomes the *olfactory lobe.* The vertex of this angle swells out to form the bulbus olfactorius; the inner and upper branch or leg of the same runs, as the inner olfactory convolution, into the frontal end of the gyrus fornicatus, while its outer and lower branch passes, as the exterior olfactory convolution, into the temporal end of the gyrus fornicatus (gyrus uncinatus). Between the two branches of the angle lies the triangular olfactory space—the lamina perforata anterior—formed by a part of the under surface of the end of the corpus striatum covered by a thin layer of cortex tissue.

Since, after withdrawal of the olfactory lobe, the underlying form of the inner surface of the hemisphere, throughout the course of its further development, must be that of a half ring with its opening looking forwards, the origin of the *arch-like fundamental shape* of the same becomes, easy of comprehension.

This same *arch-like fundamental form* develops itself in another way from the shield-shaped unbroken surface of the hemispheric vesicle. The convex wall of this vesicle becomes cemented at one part of its surface with the outer surface of a ganglion (the nucleus lenticularis, fig. 256 *L*) which, springing from the caudex cerebri (Hirnstamm), projects into the cavity of the vesicle, and the space involved in this process of cementation is the only point where ganglion substance and the wall of the hemispheric vesicle come directly into contact with each other without being connected by means of the medullary substance of the projection-system* (figs. 266, 267, 268). This region of cementation, within whose limits the hemispheric wall remains persistently thinner than at any other part, and which is therefore overtopped by the parts around it, comes to form the *floor of the fossa Sylvii*, extends from the anterior border of the convex surface of the hemisphere, close to that part of the median ring formed by the external olfactory convolution—represented in the Human brain by a simple line of tissue which, appearing as if inlaid, forms one side of the olfactory triangle—and reaches backwards and upwards over more than half of the outer surface of the cerebrum. This fossa (which, when the nucleus lenticularis is poorly developed, is but a fissure) forms the external lumen of the *arch of the hemisphere*, which, opening anteriorly, surrounds the above-mentioned seat of the cementation between the nucleus lentiformis and the cortical substance (fig. 256 *L*). This arch is made up of an upper limb—the *frontal lobe* (*F*), a lower limb

* The medullary substance, seen in the plates and especially in fig. 256, between the outer surface of the nucleus lenticularis and the cortex of the island of Reil, does not, as will be developed later, immediately unite the two. The nerve fibres simply pass over the convex surface of the former, without entering into any closer connection therewith. (TRANS.)

—the *temporal lobe* (T), and a vertex—the posterior part, the *occipital lobe* (O).

The convex outer surface of the lens-shaped hemispheric vesicle becomes in this fashion a false arch, which has for its lumen the cul de sac of the fissure of Sylvius.

Fig. 256.

Fig. 256. *Profile section, from the brain of Circocebus cinomolgus (somewhat enlarged).* F, frontal extremity. O, occipital extremity. T, temporal extremity. R, cortex cerebri. Op, cortex of the inner side of the operculum (Klappdeckel, part of 1st primitive convolution* overhanging the island of Reil) which forms one boundary of Burdach's superior fissure, the other being formed by the cortical substance of the island. H, the ammon's horn. SH, sulcus hypocampi. L, the third member of the nucleus lenticularis. Cl, claustrum (sometimes nucleus tæniæformis, Vormauer). A, nucleus amygdalæ. Cs, tail of the nucleus caudatus†. P, tŭberculum posterius thalami optici (Polster d. Sehhügels). G, corpus geniculatum externum. pr, fibræ propriæ uniting two convolutions. arc, fasciculus arcuatus. unc, fasciculus uncinatus. lg, fasciculus longitudinalis inferior. Ca, anterior commissure. inf, inferior horn of the lateral ventricle. P_1, upper member of the projection-system.

The large size of the floor of the fossa Sylvii, *the island of Reil*, is a distinguishing mark of the highest grades of cerebral development, for the size of the island depends upon that of the nucleus lenticularis, while the latter keeps pace, in point of development, with the cerebral lobes. It is worthy of notice that this region of the cortex is also connected with the power of speech.

Following the arch-like fundamental form of the convex surface, the 2—4 primitive convolutions of the Mammalian brain develop themselves, bounded by secondary parallel longitudinal fissures. (Leuret, Huschke.) The typical brain of the Ape and of Man exhibits but three such convolutions, of which the outermost shows, however, a decided tendency to split into two, and is further characterized, 1st, by the interruption of the middle arch or convolution by the two transverse central convolutions, and 2d, by the consolidation, in the parietal region, of the middle and lower convolution-arches. (Bischoff.) The development of the convolutions of the convexity alone stands in a fixed relation to that of the hemispheres, and to that of the encephalon in general, in the respect of its highest tendencies. The entire convolution-territory, formed from the median ring, keeps pace, in its development, with the lobus olfactorius alone. The gyrus fornicatus, which, in the Ape and Man, is crowded to the inner surface of the hemisphere, and which, even there, is enclosed in its entire length by the external convolution of the convexity, presses forward, in the brains of the lower animals, at the temporal, as well as at the frontal extremity, to the outer surface. Indeed, it forms there the entire frontal end of the cerebral lobe, intruding itself in front of a transverse fissure, which, not found in the Human brain (Fig. 261

* For mode of numbering the convolutions adopted here, see page 667. (TRANS.)

† Used synonymously with corpus striatum, whereas in English works a distinction is made between them. (TRANS.)

S,) forms, with the falciform fissure, a sulcus cruciatus and covering for the lobus olfactorius, so that, in fact, behind the frontal bone of the Ape and of Man, other parts of the brain are to be found than those which lie behind the frontal bone of the other Mammals.

Such being the distribution of the cortex cerebri, it may be further observed, with regard to its structure, that 1. A common type of stratification obtains in the cortex of the convex surface of the hemispheric arch and in that part of the gyrus fornicatus which encircles the median section of the corpus callosum. As types deviating from this are to be noticed:—

2. The type of the occipital extremity.
3. The type of the fossa Sylvii.
4. The type of the ammon's horn.
5. The type of the bulbus olfactorius.

1. The Common or Five-strata Type of the Cortex Cerebri.

The most common constituent of the first stratum is the basement-substance, common to and characteristic of the gray matter of the brain, which, under a moderate magnifying power, appears as a uniformly punctated tissue, peopled, in varying degree of density, by ganglion-cells. This basement-substance is called by Rokitansky ependyma, by Virchow, neuroglia, by Kölliker, connective tissue, by Deiters, spongy tissue, by Henle and R. Wagner, fused ganglion-cell substance. Occurring in the olfactory lobe and ammon's horn, it receives from Clarke the designation of gelatinous, from Kupfer that of molecular substance. Like Henle and Wagner, who called this stratum the *central covering layer*, so also Stilling regards the tissue which is completely identical with this as a nervous tissue when it appears in the cerebellum, and sees therein nothing but a felting of the finest and longest drawn out nerve-cell processes.

While, in order to be consistent, we should assume that a quantitative relation must exist between the thing produced (the tissue under consideration) and the producers (the nerve-cells which are regarded as spinning out the tissue), the following fact, of comparative-anatomical interest, must be looked upon as an argument against such an interpretation of the nature of the substance in question, viz., that the relation, in point of thickness, between the four inner nerve-cell laden strata of the cortex and this outer stratum, which is composed essentially of this basement-tissue (Fig. 257),* is one which varies exceedingly within the limits of the Mammal series. In the Human brain, for example, this first stratum constitutes but $\frac{1}{10}$—$\frac{1}{8}$ part only, in that of the capuchin Ape $\frac{1}{6}$—$\frac{1}{7}$, of the Dog $\frac{1}{6}$, of the Cat $\frac{1}{5}$, of the Bat $\frac{1}{4}$, of the Calf and Deer $\frac{1}{3}$ of the entire thickness of the cortical substance. Its absolute thickness, indeed, which in Man is 0.25 mm., increases in the Bat to 0.30 mm., in the Calf to 0.40, and in the Deer to 0.50. These facts accord much better with the theory that, side by side with the nerve elements of the cortex, there exists a non-nervous basement-substance, which, in the noblest brain types, is overbalanced and thrown into the shade by the really active elements.

It is to this basement-tissue, which here as well as in the spinal cord is to be distinguished from the non-nervous constituent of the white substance, that the peculiar textural character of the gray substance is due. That the

* The preparations here designed were, without exception, after being hardened partly in a sol. of bichrom. pot. 2%, partly in alcohol, colored with carmine, rendered transparent with turpentine, after withdrawal of the water by means of absolute alcohol, and put up in damarlack. (Clarke's method.)

nerve cells alone could not give to the gray substance its distinguishing character, appears from the fact that they occur here and there in the medullary substance in great numbers (medullary substance of the island of Reil and of the capsula externa) without causing the parts to appear as gray substance. The greater or less intensity of the gray tint of the cortex is at the same time certainly dependent (aside from its richness in capillaries) upon the aggregation of nerve cells which act as pigment bearers, so that strata which, like No. 3 in fig. 257, are comparatively thinly peopled with the latter, appear as more or less well-defined, bright, concentric intermediate lines.

The non-nervous substance consists of an amorphous and of a formed portion. The amorphous basement portion, but slightly colorable in carmine, has (perhaps only in consequence of a post-mortem change) a turbid look, owing to the presence of dark molecular points which are found beside the branches of the finest fibres discoverable by the highest magnifying powers, and are not to be referred exclusively to cross-sections of the latter. Deiters, in strict obedience to the cell theory, refers the origin of this basement substance to a splitting up of the fused protoplasm of the formative cells, a process which probably took place at a time when the latter had not yet separated themselves into nervous and non-nervous elements. As formed cell-

Fig. 257.

Fig. 257. *Transparent section from a sulcus of the 3d frontal convolution. Man.* (Enlarged 100 times.) 1. Stratum of the small dispersed cortical elements. 2. Stratum of the small, closely packed pyramidal cortical elements. 3. Stratum of the large pyramidal cortical elements (Ammon's horn formation). 4. Stratum of the closely packed cortical elements (granule-like formation). 5. Stratum of the spindle-shaped cortical elements (claustrum formation). *m.* Medullary substance.

equivalent elements belonging to this tissue he recognizes, in the cortex cerebri, only free nuclei. I must, however, insist upon the indisputable fact of the occurrence here of the star-shaped cells, with *very little protoplasm*, and a *great number of the finest possible processes*, such as he acknowledges to occur in the kindred stroma of the gelatinous substance of the spinal cord and oblongata, a fact which accords with Kölliker's views with regard to the nature of this substance. Extremely delicate in the natural state (simulating free nuclei), these cells swell up under certain pathological conditions and assume grotesque forms. This takes place, for instance, in a hyperæmic condition when, owing to the narrowing of the perivascular space by the distended vessels, the drainage of the interstitial serum is interfered with, and to a still greater extent in cases of degeneration of the lymph glands of the head and neck. Bodies of the same kind are those which, from the borders of the perivascular lymph spaces, throw the bridge-like threads (described by Roth) across the gaps. According to this explanation, the basement substance of the gray matter is traversed by a network made up of the processes of non-nervous cells. The nuclei of these cells measure 9–10 μ.* The surface of this first cortex stratum is invested by an extremely delicate layer, composed of the finest varicose medullary nerve-fibres, which run across each other in every direction (Kölliker). This layer of nerve-fibres is not recognizable as such in section preparations, but, as Arndt has observed, the presence of connective-tissue fibres which run parallel to the surface gives a dirty, opaque look to the but slightly colorable border of the first stratum of the cortex. This mere suggestion of a medullary layer appears on the gyrus uncinatus, developed to the far more powerful stratum reticulare. In this latter position, certainly, and probably wherever it occurs, it is made up of the outwardly directed ganglion-cell processes. Through the entire thickness of the outer stratum of the cortex are scattered angular, irregular *nervous elements* with forked processes. They are characterized as such, according to the just criterion proposed by Deiters, by the presence of a relatively considerable protoplasm, recognizable at the first glance.

If we hold in mind the manifold ramifications of the nerve-cell processes, discoverable by careful inspection, and the already proven instances which may fairly be considered as typical of anastomoses between processes of cortical cells (Arndt, Besser), we are led to the further assumption of the existence of a network of nerve-fibres embedded in the gray basement substance, and forming the third diffused constituent of the same. The considerations which reconcile the assumption of such a general anastomotic fusion in the region where the medullary nerves take their rise, with that of the isolated conduction, were brought forward on p. 651. In concluding the discussion of the general characteristics of the gray substance of the brain, mention may be made of the fact that the nerve-cells appear as sharply defined elements in the gray fibrous network, at least as early as the fifth month of development (Arndt). They are unmistakably defined as the permanent elements by the parallelism of their axes with the nerve-fibres of the corona radiata, an arrangement which (*v.* fig. 257, 3) is so characteristic of the structure of the cortex.

In spite of the recognition of the existence of these cells at such an early period of development, Arndt considers himself justified in confirming the statement made by Bessers, that at the time of birth the nerve-elements have degenerated to the transition state of nuclei surrounded by an ill-defined

* $\mu = \frac{1}{1000}$ millimetre.

mass of fibrous twigs (uncontouririten Reisernetzen), and that the central part of this mass becomes afterwards transformed again, as it were, to protoplasma. I feel obliged to consider this surprising conclusion as surely not deduced from a study of typical specimens, for on section preparations from the cortex cerebri of new-born Children, the most characteristic permanent forms, and their universal distribution, are too unmistakably and easily demonstrated.

The structural variations between the different concentric strata of the cortex depend, first, on the differences in the density of distribution, and, second, on the differences in the form of the nervous elements. The pyramidal form (fig. 258, *a*, *b*), the only one recognized by many observers (Luys, Arndt, Stephany), is the predominant form within the five-strata type, being represented in its second stratum by small, closely crowded elements, 10 μ in height, and in its third by cells which, as they pass toward the interior, constantly increase in size till they attain a height of 40 μ, at the same time always increasing their distance from one another. If it be called to mind that the roots of the anterior spinal nerves are connected, at their origin, with elements which, through the slenderness of their body, the gradual character of its transition into the protoplasm of the processes, and the great number and size of the latter, are sharply distinguished from the inflated cells of origin of the posterior roots, scantily provided with rather slender processes, it is impossible not to recognize the existence of a morphological relationship between the pyramids of the cortex and the former of these cell-elements just referred to, a relationship which embraces the cells of origin of all the cerebral motor nerves, and which justifies us in drawing a conclusion by analogy as to the signification of the pyramids of the cortex. The larger elements of this third stratum, inasmuch as they represent the

Fig. 258.

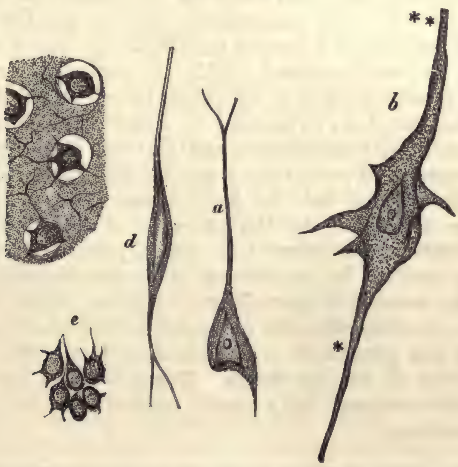

Fig. 258. *a*, Common mutilated form of pyramid, with angular nucleus and forked axis-process. *b*, True form of the elements of the second and third strata of the cortex, represented by one of the large cells of the ammon's-horn formation with angular nucleus. **, The curtailed axis-process. *, The middle base-process. *c*, Elements of the fourth stratum of the cortex. *d*, Spindle-shaped cortical element of the fifth stratum, with spindle-shaped nucleus. *e*, Elements of the so-called kernel-stratum of the cortex cerebelli.

cells by which the ammon's-horn is almost exclusively peopled, receive the name of *ammon's-horn formation.*

The simple pyramidal form (fig. 258, *a*) under which the cells are most commonly to be seen is a deceptive form. Their true shape (fig. 258, *b*) is that of a spindle whose long axis lies in the same direction with the radiating fibres of the medullary substance of the convolution. Towards the outer surface of the cortex this spindle-cell runs out into a powerful *external* (and, according to M. Schultze,* a branched) process, which, remaining (according to Koschewnikoff) undivided, represents the axis-cylinder process as described by Remak, M. Schultze, and Deiters. From the thickest part of the spindle there pass off lateral branching-processes, to the number of 5—7, which, as well as the external terminal processes, have been proved to anastomose with other processes. The designation of cortical pyramid being accepted, we may distinguish the three varieties of process as 1st, the apex-process; 2d, the central base-process; 3d, the corner base-process.

The central base-process, being rarely found in the Human brain, is held by Arndt to be a monstrosity, while in the brain of the Rat and the Sheep he considers its occurrence as regular. The reason of its less frequent appearance is this: that being destined to pass into a fibre of the medulla, the direction of its course is determined by that of these fibres, which by no means run in the same straight line with the apex-process. In sections, therefore, made by cuts laid parallel to that surface of the cortex which is obtained by simply breaking hardened preparations grained in parallel lines by the radiating apex-processes, the process in question must often be lopped off, and the greater be the thickness of the entire hemisphere, and the more distant the ganglionic end of the medullary projection-fibre concerned, from its cortical end, the more likely is this lopping off to occur. Perhaps the great brittleness which characterizes the axis-cylinder processes, is the cause of their not being more often obtained by preparation with needles (Zupfpreparate).

The nerve-cells of the cortex are devoid of membrane; and Max Schulze has observed on their protoplasm also the granulated fibrous structure described in Chapter III. The younger the subject, and the greater the probability that his brain is in a normal condition, the more rarely are round or oval nuclei to be found enclosed within the protoplasm of the pyramids, or in that of the spindle-cells to be described later. Instead of being round, the nuclei are angular, *i. e.*, pyramidal or spindle-shaped, according to the form of their respective protoplasms, and run out into sharp ends (fig. 258 *a*, *b*, *d*). The corners and points often project into the cell-processes, which does not favor the opinion held by Arnold that the nuclei, originally bladder-shaped, were remodelled by the pressure of the protoplasma into its own form. If Beale's description of an optically-dense layer of protoplasma surrounding the nucleus, be considered in connection with that given by M. Schulze of the concentric protoplasmic fibrillæ, which converge toward the cell-processes, another valuable argument is furnished for the fact of the existence, within the pyramidal or spindle-shaped cell, of a smaller, denser pyramid or spindle of similar shape. Being itself a part of the protoplasm, this angular enclosed body would naturally extend into the protoplasm of the processes.

For my own part, without offering any interpretation thereof, I have objectively satisfied myself of the common occurrence, throughout the entire central system, of angular nuclei in the nerve-cells which take the form of the surrounding protoplasm, and Dr. Ernst Fleischl has kindly shown me sections from the spinal cord of the Fish which contained the same nuclei forms as I had observed in the Human spinal cord.

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* Chap. III., p. 139.

The nucleoli appear round and glistening, and in carmine preparations, by force of contrast, surrounded by a bluish-green border.

The fact that kernel-like and spindle-shaped forms, in addition to the pyramidal, are to be found in the cortex cerebri, was known even to Berlin. I have already shown that these forms, among which a certain number of the larger pyramids are interspersed, give to the 4th and 5th strata of the cortex their distinguishing characteristics. The elements of the 4th stratum (fig. 258 *b*) are either irregular (8 to 10 μ in length), or, more rarely, triangular, or elongated in the direction of the course of the radiating nerve fibres (fig. 258 *c*). These elements are more closely crowded than are those of the neighboring 3d and 4th strata.

They call to mind the nerve-elements which people the inner-granular stratum of the retina, and the gelatinous substance from which the greater root of the quintus takes its rise.

The peculiar elements of the 5th stratum, the spindles 30 μ in length (fig. 258 *d*), are to be found the most free from admixture with other forms in the inner half of this stratum, and also scattered through the medullary substance (*m*) in the neighborhood. At the summit of the convolutions these spindle-cells stand on end, parallel to the pyramids, but around the sulcus between two convolutions they lie flat (fig. 257, 5), so that the pyramids stand as it were perpendicularly upon them. Just as the pyramids lie in the direction of the course of the projection-system fibres, so the spindles of the 5th stratum, in virtue of their twofold position, lie exactly in the course of the fibræ arcuatæ, which, in passing the sulcus between two convolutions, cross the path of the projection-system fibres, becoming again parallel with them in the convexity of the convolution.

This disposition of the spindle-cells justifies us in regarding them as articulating cells of the association-system (v. p. 655). They deserve also the designation *claustrum-formation*, because, as will be shown below, the claustrum presents forms of just the same kind with these, though more compactly disposed.

These cells should not, however, on account of their spindle form, be regarded as bipolar cells; for it is evident that they send out lateral processes, which, however, appear to me to be collectively directed toward the surface of the cortex, and therefore not to effect an immediate connection between these cells and the projection-system of the medulla.

The medullary substance of the convolutions gathers itself, even within the limits of the cortex, into recognizable radiating bundles, which are to be seen on section preparations, from the inner half of the 3d stratum onward, separating the cell-masses, in their passage, into columnar groups. The division of a medullary fibre within the cortex (or rather its formation out of the processes of two cells) I have seen once with distinctness. On the other hand, a union of the fibres into a network, which Stilling describes as occurring in the cerebellum, certainly never takes place in the medullary substance of the convolutions. Fibræ arcuatæ, as well as fibres of the radiate system (corona radiata), are to be found embedded in the gray matter of the cortex. They occur, however, but rarely, and I have never been able to find them so densely disposed as to be visible to the naked eye under the form of bright (devoid of pigment) concentric lines (Kölliker). The nerve fibres of the cerebral lobes are fine, varying in diameter, according to Kölliker, from 2.6—6.7 μ. The connective tissue of the medullary substance is made up of a reticulum of rather large connective-tissue cells, furnished with thick processes, and simulating free nuclei more rarely than do the corresponding

cells of the cortex. They are ranged parallel to the nerve fibres. Finely-granular basement substance seems to be wanting to the fully developed brain, but during the period of evolution it is present, and probably gives rise to the rather gray than medullary look of the immature brain.

2. *At the extremity of the occipital lobe*, and within the neighboring sulcus of the median surface, *the sulcus hippocampi*, corresponding to whose concavity there is a convex elevation which projects as hippocampus minor on the thin inner-wall of the posterior horn of the lateral ventricle, a structural type of another kind prevails. No longer the pyramids, but the kernel-like bodies are here the ruling forms (Körnerformation). The pyramids constitute only one stratum (the 2d) which contains cells of moderate and about equal size, and thus the forms of the former 4th stratum, as it were, appear here as the 3d. This broad and crowded 3d stratum, however (Kernelformation), is split up by the insertion of two barren (thinly-peopled) intermediate strata (kahle Zwischenkörnerschichten), so that a zone results made up of five different layers of tissue, within which the kernel-like formation (which occurs but once in the first-described structural type) appears three times. Upon the innermost kernel (or granular)-stratum there follow the spindles.

This cortex type is thus made up of eight strata. The two barren intermediate strata seem to blend together, and appear as a single, perfectly constant stripe (rendered white by the absence of pigment), which in this region is defined with an unusual sharpness, and the intervening granular stratum, by reason of its narrowness, is lost in the general effect. Within these thinly-peopled strata are to be found, occurring either alone or in small, widely-separated groups, pyramids of the very largest size, twice as large as those of the ammon's-horn (solitary cells). In the Ape's brain, which is characterized by excessive development of the occipital lobe, the limits of distribution of the structural type just described are wider than in the Human brain.

Clarke took this formation of the occipital extremity as the typical structure of the cortex, and describes, recognizably, the two barren strata. Since however he, as well as many other authors, does not regard the granules (Körner, kernels) and the spindles as distinct forms, he describes the outer and inner strata of the granular formation as parts of the neighboring pyramid- and spindle-layers respectively, and reckons in conseqnence but 6 cortical strata instead of 8.

3. In the *type of the fossa Sylvii*, the third form of the cortical cell, *the spindle* attains to predominant development, as is to be seen in the claustrum, and in the nucleus amygdalæ. The claustrum, which is as it were a layer of the innermost stratum of the cortex, cut off from the main body of the same and separated from the nucleus lenticularis by the thin layer of medullary substance of the capsula externa (fig. 256, 266, 268 *Cl.*), lines the convolutions of the island of Reil, and accompanies, in fan-like folds, their curves. Having passed the limits of the island, the claustrum bends over into the cortex-wall which surrounds the fossa Sylvii, upwards into the operculum (frontal end of 1st convolution *), downwards into the 1st temporal convolution. At the same time it stretches itself forward (as shown in fig. 256), bent into the form of a clamp, into the frontal and into the temporal ends of the convolution arch which surrounds the fossa Sylvii (erster Urwindungsbogen).

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* For method of numbering convolutions, see next paragraph. (Trans.)

The cul de sac of the fossa Sylvii, together with the false arch (v. p. 658) which encloses it like a wall, a district defined and consolidated to a morphological unit by the claustrum, and which finds its analogy in all Mammal brains, constitutes the form-determining centre of the convexity of the cerebrum. Not only therefore did Leuret, as the discoverer of the typical disposition of the convolutions, have a right to create a terminology therefor, but also, as has just been shown, that method is the true one which takes the region in question for a central point in numbering the convolutions.* Huschke, in his valuable work, followed Leuret's lead. This mode of numbering does not, like that which has been popular since the time of Wagner, lead to the morphological absurdity involved in destroying the unity of the convolution-arch marked out by the claustrum (the 1st original convolution), by dividing it like patchwork into a 3d frontal and a 1st temporal convolution, and further in designating the so well defined inferior frontal convolution with a different number in different animals; for the number of the frontal convolutions, and, in consequence, the designating number of the lowest, varies within the Mammal series between 2 and 4.

The claustrum appears on cross sections of the frontal lobe under the form of a bent cone with its base turned downwards. This thickening of its lower part is most strongly marked where, crossing the base of the island,

Fig. 259.

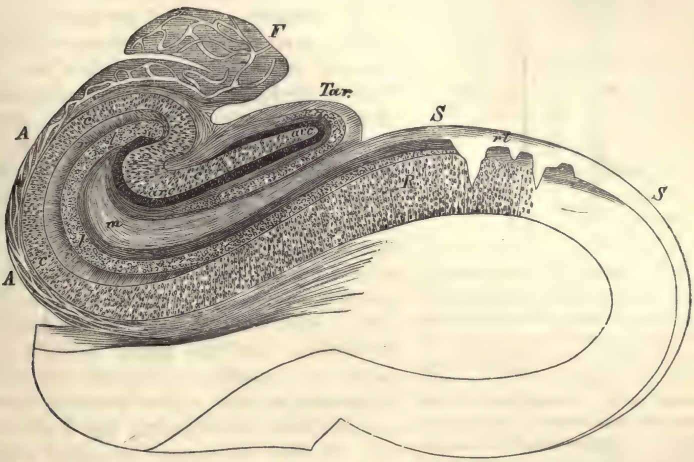

Fig. 259. Transparent section from the Human ammon's horn; from the middle of its length (5 ×). *S*, subiculum cornu ammonis. *Tar*, fascia dentata Tarini. *F*, fimbria; *A*, alveus; *cc*, stratum convolutum, containing the large pyramidal elements; *r*, stratum radiatum; *l*, stratum lacunosum; *m*, lamina medullaris; *rt*, substantia reticularis; *arc*, layer of the crowded nerve-cells in the fascia dentata; *R*, cortical substance of subiculum. [*arc* in this fig. refers to the dark layer over which these letters stand. TRANSLATOR.]

the claustrum enters the temporal lobe. Here appears a rounded mass (the nucleus amygdalæ fig. 256 *A*), having the same structure with the claustrum, to the base of which it is connected by means of transition masses, which may be considered with equal justice as belonging to the latter or to the former. This mass forms the anterior wall of the inferior horn of the lateral ventricle (fig. 256 *inf.*) The *entire spindle-cell formation* which,

* So that the convolution immediately surrounding the fossa Sylvii is called in its whole length 1st convolution, etc. (TRANS.)

spread out along the walls of the fossa Sylvii, finds its termination in the amygdala, *may be conceived of as distributed in the form of a fan, unfolded in a plane parallel to the surface of the island. Its edges are bent over (to enter the 1st primitive convolution-arch, as described) and its handle terminates in a ball-shaped body, the nucleus amygdalæ.*

That this formation should not be reckoned among the ganglia as "corpus striatum externum" (Arnold) is shown by its connection (to be further developed below) with the fibræ arcuatæ of the hemispheres, which latter are characterized by being associated exclusively with cortical substance.

The fact that the cortex cerebri passes in unbroken continuity over the nucleus amygdalæ, gives the latter the deceptive look of being part of an entirely foreign formation, the ammon's horn, which it assists to form the so-called hook of the gyrus fornicatus (gyrus uncinatus).

Fig. 260.

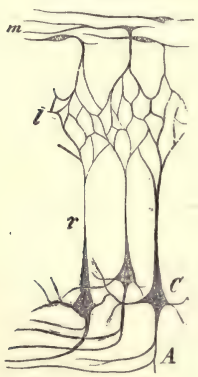

Fig. 260. Scheme representing structure of the stratum convolutum of the ammon's horn, together with the medullary substance of the alveus and of the lamina medullaris; *m*, lamina medullaris with its very small nerve-cells, = stratum 1 of the five-strata cortical type; *l*, region of the stratum lacunosum, with a network formed of the apex-processes of pyramidal cells, = stratum 2; *r*, stratum radiatum, which corresponds to the outer half of stratum 3; *C*, pyramids of stratum convolutum, corresponding to inner half of stratum 3 of the above-mentioned cortical type; *A*, alveus, = medullary substance of the convolutions, belonging to the projection-system, which in this region, through failure of the kernel and spindle strata, is brought into direct connection with the pyramid stratum *C*.

4. *The ammon's horn formation.* The temporal end of the gyrus fornicatus, the gyrus uncinatus, or subiculum cornu ammonis, together with the ammon's horn itself, has been shown (p. 658) to be a part of the primitive ring of the median hemispheric surface, around whose lumen the cortical substance ends with a free edge. This free edge, throughout the greater part of the length of the ammon's horn, is rolled inward upon itself, so as to form an *S*-shaped curve. The starting-point of this curve is (*v.* fig. 259) the convolution *S*, the *subiculum cornu ammonis.* Upon the latter lies the free edge of the cortex mentioned above, folded back to the starting-point to form the *fascia dentata Tarini* (*Tar*) (the beak of the *S*). Between the subiculum and the fascia dentata, is disposed in unbroken continuity the cortical substance of the rolled stratum (stratum convolutum *c c*), forming the body of the *S*. Its first curvature, invested with the (*AA*) medullary substance of the alveus (Muldenblatt), forms a rounded prominence on the inner wall of the inferior cornu. The membranous medullary substance of the alveus gathers itself into a cord-like mass, the fimbria (*F*), the principal origin of the fornix. This cord forms the third of the four longitudinal prominences of the ammon's horn, represented here in cross-section, whose development finds its explanation, morphologically speaking, in the process of involution just described. The subiculum receives a network-like medullary investment analogous to the medullary veil, so to speak, which covers the cortical surface of the rest of the brain, but far more strongly developed than that is, in the form of the *substantia reticularis* (Arnold) (fig. 259 *rt*). This medullary investment appears also on what, except for the involution process,

would be the free surface of the stratum convolutum, filling in reality (as is to be seen in fig. 259) the fold between the subiculum and fascia dentata, where it forms the lamina medullaris (Kernblatt) (m).

This involution of the cortex of the ammon's horn, which takes place in a horizontal plane, seems unable to account for the apparently longitudinal crook by which the uncus is formed. This hook-like form is produced as follows. At the anterior extremity of the ammon's horn the S-shaped stratum convolutum unfolds itself, retaining only the form of a gently undulating curve, the prominences of which appear in relief, as the so-called claws (digitationes pedis hippocampi majoris). Thus unfolded, the free border of the stratum convolutum (as seen from within, *i. e.*, from the median line) projects for a short distance above the surface of the subiculum, forming the point of the hook, while the nucleus amygdalæ, thrust in in front of the ammon's horn (fig. 256 H, A), rounds off the extremity of the gyrus uncinatus. (This makes it appear as if bent longitudinally upon itself, thus giving its curve to the hook, of which, as has been said, the subiculum cornu ammonis forms the long arm, and the projecting stratum convolutum the short arm and point.—TRANS.)

The ammon's horn is, only as regards its gross conformation, a less simple structure than are the other convolutions; as regards its textural stratification and the variety in form of its cells it is the simplest of the cerebral convolutions, a defective formation containing, of all the cortical forms, that of the *pyramid* alone.

Even in the cortical substance of the subiculum, the pyramids of greater and less dimensions are the only forms to be found. Absence of the spindle-cell formation deprives the different parts of the cortex in this region of one of their means of mutual communication, but at the same time, in compensation therefor, as it were, the membrana alba involvens, which furnishes the other means of mutual communication, and which is so scantily developed over other regions of the cortex (*v.* p. 662), appears, on the surface of the subiculum, much more fully developed, as the substantia reticularis (fig. 259, *rt*). The external contour of the 2d stratum of the cortex in this region appears here and there defective (fig. 259, S–S) by reason of the passage of the apex-processes of large pyramidal cells, which even Arndt acknowledges to divide into branches in this region, running in bundles to carry their contingent to the formatio reticularis. The stratum convolutum in the interior of the ammon's horn proper (c, c, $c_{,}$) is made up exclusively of the very largest pyramidal forms, viz., of such as characterize the *inner half* of the 3d stratum of the cortex. Finally, in the region of the *fascia dentata* appear the smaller forms, closely crowded together in a manner peculiar to this formation; for in the other parts of the cortex they lie at an average distance of 100 μ from each other. (*Stratum corporum nerveorum artorum, arc.*). To this density of their distribution it is to be ascribed that *Kupfer*, *Kölliker*, and *Deiters*, overlooking the delicate and therefore indistinctly-outlined protoplasm which covers them, observed in this cell-formation only those nuclei which are invariably bladder-shaped. The connectile *stratum granulosum*, described by them, does not really exist as such, and that which was erroneously so called consists, as Arndt correctly observed of the protoplasm, of nerve-cells. In the structure of the ammon's horn, which is defective as regards its nerve elements, the stratum of the non-nervous basement substance is represented in its full breadth, as is diagrammatically represented in fig. 260 (to be compared with fig. 259). By following the external contour of the cortex of the subiculum we come to the lamina medullaris (Kernblatt), which represents the external layer of the typical cortex enclosed in the fold made by the stratum convolutum; the 1st cortex-stratum (m). The small scattered cells of this stratum are

generally difficult of recognition, and lie parallel to the course of the fibres of the lamina medullaris.

The 2d typical cortex-stratum to which the small pyramids are wanting is represented by the stratum lacunosum (l) (stratum reticulare of Kupfer). The gaps, indicated at l, fig. 259, represent perivascular spaces which form a close network about a system of anastomosing capillaries, within which latter system the vessels of the lamina medullaris, coming from the pia mater, meet and join those coming from the ependyma on the ventricular surface which belong to the medullary substance of the alveus (AA). In this stratum the axis-processes of the pyramids anastomose to form a nervous network (as represented in the diagram).

3. The place of the outer half of the 3d typical cortex-stratum, whose pyramids of middle size are here not represented, is supplied by a layer of tissue characterized, as Kupfer observed, by being ruled in parallel lines by the long apex-processes of pyramid cells (stratum radiatum). Next follow the pyramids of the inner half of the 3d cortex-stratum, which, disposed in several layers one above the other, constitute the characteristic formation of the ammon's horn (c). The gaps which are often to be seen around the individual nerve-cells, and the formation of which is usually ascribed to a retraction of the tissue consequent on the process of hardening, are especially noticeable around these large pyramids, and are looked upon by H. Obersteiner as *pericellular lymph channels.* He even succeeded in injecting them, and saw them on section preparations, opening into the perivascular spaces, and containing bodies which he regards as undeveloped lymphoid elements.

The 4th and 5th strata of the regular cortex-type are, in the Human ammon's horn, devoid of non-nervous substance, while in that of certain animals (Cat, Rabbit) a layer of this substance is certainly present (Kupfer's stratum moleculare). This accounts for the fact that the immediate union of the alveus with the pyramid-cells, which takes place in the Human brain, escaped Kupfer's notice, since this union is brought about in animals by means of his stratum moleculare. The alveus (A) is made up of the medullary substance belonging to the cortex of the ammon's horn, and, like other parts of the medullary substance of the hemispheres in similar positions, it is invested with an epithelial lining, that of the lateral ventricle. Clarke has described the epithelium of the cavity of the bulbus olfactorius, declaring it at the same time to be identical in kind with that lining the central canal of the spinal cord, as belonging to the palisade variety, and tapering off into thread-like prolongations which connect with certain kernel-like bodies, placed, by Stilling only, in the category of nervous elements. I believe this variety of epithelium to be characteristic of the ependyma of the brain wherever it occurs, and have convinced myself thereof so far as the surfaces of the corpus striatum, thalamus opticus, and corpus callosum are concerned, while Gerlach has traced cylinder-epithelium to within the aqueductus Sylvii. With regard to the pavement epitoelium, reported by other observers as having been found in the ventricles, it is to be remarked, 1st, That the evidence obtained from a bird's-eye view of the epithelium is not conclusive; and 2d, that in making thin sections perpendicular to the surface it easily happens that the delicate extremity of the epithelial cell is cut off, together with its thread-like prolongation, as was mentioned with regard to the processes of the nerve-cells of the cortex. The walls of the camera septi pellucidi, like the median surfaces of the hemispheres to which they in reality belong, are devoid of epithelium.

5. *The formation of the bulbus olfactorius.* The anterior half of the ring

formed during the evolution period by the median surface of the hemisphere (*v.* p. 658) becomes the olfactory lobe, which receives, in the Human brain, the inappropriate name of the olfactory nerve. It consists of a diverticulum from the hollow globe of the hemisphere, is itself hollow like the

Fig. 261.

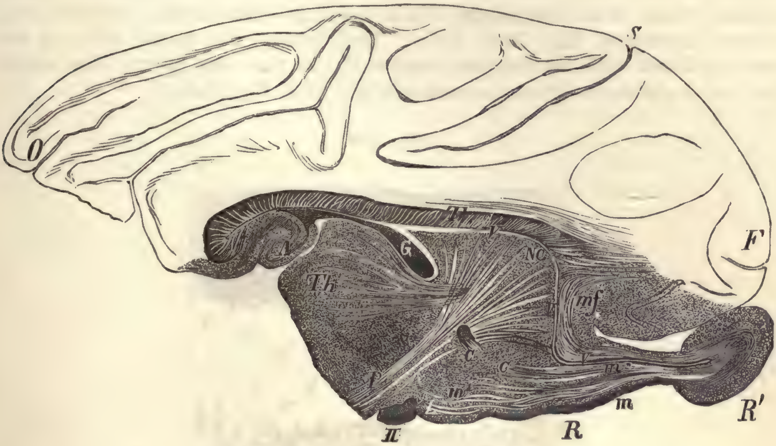

Fig. 261. *Transparent profile section from the brain of a Dog.* *FO*, cerebral lobe; *S*, transverse branch of the sulcus cruciatus of Leuret. (v. p. 658, gyrus fornicatus in the lower Mammals); *F*, frontal lobe, formed by the gyrus fornicatus; *R*, lobus olfactorius; *R'*, bulbus olfactorius; *VV*, cavity of lobus olfactorius in communication with the lateral ventricle; *CC*, the portion of medullary substance of the olfactory lobe that is destined to enter the anterior commissure, and the section of the anterior commissure which stretches out to meet the nerve fibres in question. The entire course of this group of fibres has the shape of a curve with its convexity turned outwards, and the summit of this curve lies outside of the section; *m*, medullary substance of the bulbus olfactorius; m^1m^2, medullary substance of the olfactory lobe, destined for the corpus striatum (nucleus caudatus); *L*, inferior surface (Basaltheil) of the nucleus caudatus (region of the anterior perf. space); *NC*, head of the nucleus caudatus, which reaches by an arch-shaped course the infer. surface (Basaltheil); *P*, part of the basis cruris cerebri derived from the nucleus caudatus; *Th*, thalamus opticus, in connection with groups of fibres which come from the cortex of the frontal lobe; *II*, nervus opticus; *G*, fornix; *T*, corpus callosum (trabes. cerebri); *A*, ammon's horn; *mf*, medullary substance from the olfactory lobe describing a curve to enter the gyrus fornicatus.

cerebral lobes, and its cavity even communicates with the lateral ventricle (fig. 261, *V*). Its cortex is directly continuous, superiorly, with that of the rest of the brain. Inferiorly and posteriorly (towards the lamina perforata anterior) its border would constitute a portion of the free edge of the cortical substance surrounding the lumen of the primitive ring (*v.* pp. 658 and 668, ammon's horn), did not the lamina perforata anterior spread a layer of cortical substance (as will be explained below) over the under surface of the end of the corpus striatum, thus prolonging the cortical substance of the olfactory lobe.

The bulbus olfactorius, from whose outer surface the nerves of the *Schneiderian* membrane pass off, has the form of a cap set upon this conical projection of cortical substance, the olfactory lobe (fig. 261, *R'*). From its concave interior springs a special independent medullary system, which in-

vests the anterior surface of the olfactory lobe, divides itself into two parts to accompany the external and internal olfactory convolutions, and gives to them, when looked at from below, the deceptive appearance which caused the olfactory lobe to be regarded as a nerve (*m*).

Along the sides of the anterior perforated space run the two divisions of the olfactory lobe, the *external and internal olfactory convolutions.* The former is continued into the frontal extremity of the gyrus fornicatus, beneath which it is recognizable for a certain distance as a distinct longitudinal elevation (fig. 264, *Rt'*). The latter, the larger of the two, becomes fused with the temporal extremity of the same gyrus, the subiculum cornu ammonis (gyrus uncinatus) (fig. 265, *Ra, Sub.*).

Fig. 262.

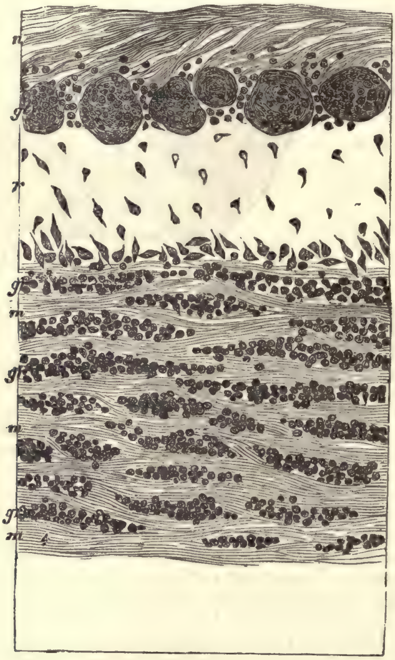

Fig. 262. Transparent section from the bulbus olfactorius of an Ape (100 ×). *n*, stratum of the olfactory nerves; *gl*, glomeruli olfactorii; *r*, cortical substance, whose ganglion-cells are most closely packed towards the inner border (stratum gelatinosum; *gr*, kernel strata; *m*, medullary strata.

The bulbus olfactorius, whose structure Luys justly compares to that of the retina, receives the nerves which have their peripheric extremity in the olfactory cells of the nasal mucous membrane, as an abridged projection-system, just as in the retina the projection-system is represented by a still shorter tract, that which connects the rods and cones which represent the special terminal structures with the nervous elements which represent their centres.

These olfactory nerves (fig. 262, *n*) pass into the so-called *stratum glomerulosum* (*gl*), made up of rounded masses, the glomeruli, which are sur-

rounded by, and to some extent filled with, small nuclei-like cells. They contain further convoluted vessels, but consist, for the most part, of a finely granular substance resembling the basement-substance of the cortex cerebri. The true nature of these masses of origin of the olfactory nerves, which were first observed by Leydig in the Fish, can be appreciated only in Man (fig. 263), where the connective substance is wanting, which, in animals, distends the glomerulus olfactorius to its great size. The formation seems to consist here simply of an olfactory-nerve fibre, wound into a knot by the aid of the cells inserted in its course. The non-nervous substance, the scantiness of which is characteristic of the structure of the Human brain, as was shown above in treating of the ammon's horn, and of the cortex in general, is positively wanting in the glomeruli in question, for which reason the view taken of their structure admits, in such brains, of being satisfactorily established, which is rendered impossible in the brain of the lower animals, by the distention of their olfactory lobes with this indifferent substance, by which the curvatures of the knot must be forced apart from one another and straightened out.

Fig. 263.

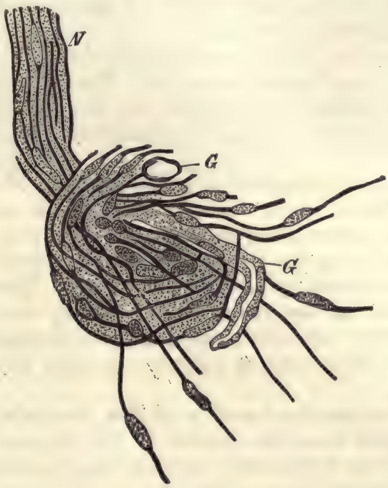

Fig. 263. A glomerulus olfactorius from the Human brain; *N*, the entering olfactory nerve; *G*, blood-vessels. (600 ×.)

The 3d stratum, *Clarke's stratum gelatinosum*, contains in its more external portion, scattered toward its inner surface, rather densely disposed nerve-cells, which are sometimes of a spindle, sometimes of a pyramidal shape, and are embedded in the basement-substance common to all regions of the cortex. In the medullary substance of the bulbus which comes next in order are to be seen arranged in alternating concentric layers, bundles of nerve fibres, and small, closely packed nerve-cells, bearing a close resemblance to the granules of Purkinje in the cerebellum: strata granulosa and medullaria (*gr*, *m*). These small, irregular nerve-cells differ only in size, perhaps, from the granules of the retina, and the elements of the fourth stratum of the cortex cerebri in general.

The cortical substance of the lobus olfactorius, apart from that of the

bulbus, has not yet been described with monographic accuracy. It seems to be made up of large cells of a single type, perhaps like those of the ammon's horn.

The increase in the development of the vaulted convolution (gyrus fornicatus) which accompanies the increase in the development of the olfactory lobe (as seen in animals), finds expression in an enlargement of the ammon's horn, which stretches itself horizontally forwards, beneath the splenium corporis callosi (figs. 261, 264, 265 *A* and *Ah*), so as to cover the thalamus opticus, while in Man, at a corresponding part of its course, it lies behind this ganglion. This exuberance of development causes the ammon's horns of the two sides to become fused together in the median line (posteriorly), and the two halves of the fornix, in like conditions, become similarly united throughout the length of its trunk. In like manner the septa pellucida, whose development is also bound up with that of the olfactory lobe, become thickened and fused together, to the occlusion of the so-called ventricle between them. The latter fusion is to be found even in the Ape, so that (it may be with the exception of the primate Apes) it is only in Man that the hemispheres are united solely by the corpus callosum and anterior commissure.

In these different territories of the cortex the *entire medullary substance of the cerebral lobes* takes its origin. A satisfactory demonstration of the relations of the various parts of the latter has not yet, even approximately, been given. The facts which are worthy of notice in this connection are exhausted in the following remarks.

The general divisions of the medullary substance have already been referred to in the introductory remarks. These divisions are: 1st, the fibræ arcuatæ (association-systems); 2, the trabecular system; 3, fibres destined for the cerebellum; 4, the projection-system; 5, the commissura anterior.

In fig. 256, at *pr*, is represented a typical example of the junction of two neighboring convolutions by the fibræ propriæ which surround, in festoon-like arrangement, the intervening sulcus. At *arc* are to be seen bundles of fibres which run parallel to the long axis of the cerebral lobes, from the occipital to the frontal extremity of the hemisphere. These fibres belong to the important system of the *fasciculus arcuatus*, which serves to unite together the most widely separated regions of the cortical substance of the convexity. Some of these bundles traverse, on their way, the upper part of the claustrum.

Further, at *unc*, appear the bundles of the *fasciculus uncinatus*, which take the shortest path from the frontal to the temporal extremity of the cerebral lobe, the course which they describe being concentric with, and included within, the longer course described by the fibres of the fasciculus arcuatus, which latter unites together all the intermediate regions between the same terminal points just mentioned. The fibres of the fasciculus uncinatus traverse freely the substance of the claustrum, as well as that of the nucleus amygdalæ. The anterior cord-like and hook-shaped part of the fasciculus uncinatus is joined by bundles of fibres distributed, as it were, in layers which pass through, and along the surface of, the claustrum, constituting an important part of the medullary substance of the island (of Reil) and of the external capsule (capsula externa). These fibres are connected with the spindle-cells of the claustrum formation, just as the fibræ arcuatæ in general, throughout the cortex cerebri, are connected with cells which correspond to those of that same formation; in this region, however, corresponding to the above-mentioned development (p. 666, type of the fossa Sylvii) of the innermost stratum of the cortex to an independent structure, the fibræ arcuatæ (Associations-systemen) associated with it are unusually largely represented.

At *lg* in the same figure (fig. 256) are to be seen fibrous bundles which, under the name of the *fasciculus longitudinalis inferior*, run from the extremity of the occipital towards the extremity of the temporal lobe. Along the median surface of the hemisphere, as is well known, run the nerve fibres of the gyrus fornicatus, embracing the corpus callosum in their arch-shaped course from the frontal to the temporal extremity, and playing, for the cortical substance of the median surface of the hemisphere, the same part as the fasciculus arcuatus does for the cortex of the convexity. To the gyrus fornicatus belongs the short tract of medullary substance figured at *m*, fig. 264.

Fig. 264.

Fig. 264. *Transparent profile section passing through the inner olfactory convolution not far from the inner surface of the hemisphere: from a Guinea-pig.* *F*, frontal extremity; *O*, occipital extremity of the cerebral lobe; *RR*, cortex; *BB*, external stratum of cortex; *S*, opening into a sulcus belonging to the inner surface of the hemisphere; *Bl*, corpus callosum; + + +, regions where association-system bundles, belonging to the cortex of the olfactory lobe and the gyrus fornicatus, intersect the fibres of the corpus callosum; *Sp*, superficial layer of medullary substance of the inner olfactory convolution; *m*, bundle of fibres belonging to the gyrus fornicatus; *Ah*, the ammon's horn; *L*, fibrous bundles belonging to the substantia reticularis of the ammon's horn, destined to form a part of the nervus Lancisii; *G*, the fornix; *P*, the septum pellucidum; *St*, pedunculus septi; *J*, junction of the substance of the corpus striatum with that of the septum, which takes place inwardly from the lamina perforata anterior; *C*, anterior commissure; *l*, ventricle; *Z*, pineal gland (conarium); Z′, the ganglion in the habenula (pedunculus conarii); *m′*, section of the medullary substance of the corpus quadrigeminum, which is continuous with that of the posterior commissure and the pineal gland; *A*, aqueductus Sylvii; *Th*, thalamus opticus; *ma*, corpus candidans (corp. albicans); *Cx*, caudex cerebri (Hirnstamm); *I*, bundle of fibres which have their origin in the habenula conarii, destined for the tegmentum cruris cerebri; *III*, nervus oculo-motorius; 8, the posterior longitudinal fasciculus (Hinteres Längsbündel); *Br*, region occupied by the crossing of the pedunculi cerebelli ad corp. quadrigem. (Bindearme); *Rl*, lobus olfactorius; *Rt*, prolongation of the cortical substance of the internal olfactory convolution passing beneath the frontal extremity of the gyrus fornicatus.

A certain portion of the medullary substance of the olfactory lobe is also to be ranked, as Gratiolet observed, with the fibræ arcuatæ, for as the cortical substance of the external and internal olfactory convolutions is directly continuous with the cortical substance of the gyrus fornicatus at the two extremities of the latter, so in like manner the medullary substance of the

former passes without interruption into the medullary substance of the latter. It is especially the long, most inferior fibres of the gyrus fornicatus that, running along the upper surface of the corpus callosum, as nervus Lancisii, serve, in virtue of their connection anteriorly with the cortical substance of the inner olfactory convolution, posteriorly with the substantia reticularis and lamina medullaris of the ammon's horn, to unite together these two regions of the cortex. Besides these, however, certain fibrous bundles are to be seen running longitudinally along the inner surface of the septum pellucidum, which originate in the internal olfactory convolution, and which, passing partly through and partly under its knee (genu), traverse the body and splenium of the corpus callosum to enter finally the gyrus fornicatus at various parts of its course. Perhaps they stand in connection with the parallel spindle-shaped cells of the septum (fig. 264 *L*, *Rt'*, + + +, *m*, *BlP*).

The superficial and the deeply-seated medullary substance of the external olfactory convolution coalesce in part with the substantia reticularis (fig. 265 *m ret*), in part with the medullary substance proper of the same convolution, which medullary substance forms a layer of no great thickness, between the cortex of the uncus itself and the nucleus amygdalæ (fig. 265, m^2+mf). Following the path taken by these fibres, a process of the claustrum thrusts itself into the medullary substance of the external olfactory convolution, and thus the latter by way of the spindle cells of the claustrum is brought into connection with the extensive association-systems of fibres which surround the fossa Sylvii (fig. 265 *m' Cl*).

2. As regards the *system of the corpus callosum* (trabecular system), microscopic examination of cross-sections from small Mammal brains, among which that of the Bat has been made the subject of careful investigation by Oellacher, confirms the opinion expressed by Arnold, that the corpus callosum is made up solely of commissural fibres, connecting symmetrical territories of the cortices of the two hemispheres, and not, as Foville wished to prove, of fibres of the projection-system, crossing the middle line to enter the ganglia of the opposite side. It appears also that its fibres are not distributed, as Burdach thought, exclusively to certain groups of convolutions, but, in common with the fibres of the projection-system, to all parts of the cortex. In this way the fibres of the projection-system become intimately interwoven with those of the trabecular system (Arnold, Reichert). The splenium corporis callosi is not a solid mass, but consists of two laminæ (fig. 264), to form which, it folds longitudinally upon itself, and these two laminæ, separating somewhat from each other in their course towards the temporal lobe, leave between them the clefts called respectively the posterior and the inferior horn of the lateral ventricle (Luys). The upper lamina of the splenium comes to form also the outer ventricle-wall, the tapetum (Reil) (fig. 266, *T''*). The foreign bundles of fibres, which form an intricate and delicate network with those of the corpus callosum proper, may be traced microscopically without the least danger of their being confounded with connective-tissue fibres, or with vessels (fig. 264). Among them (as Arnold has already stated) are bundles which run from the posterior part of the gyrus fornicatus to the fornix, spreading themselves out over the lower half of the surface of the septum pellucidum (fig. 264 *G*).

4. *The principal mass of the projection-system*, the corona radiata, is enclosed, at the convexity as well as at the inner surface of the hemisphere, by the above-mentioned fibrous systems, whose course begins and ends in the cortical substance. The first member of the projection-system is, however, by no means made up exclusively of radiating bundles, which (like those figured at *P'*, fig. 256, as coming from the occipital lobe) take the shortest path

to reach their destinations in the ganglia. Some of its constituent bundles, on the contrary, have an arch-shaped course, of which the most striking specimen is the fornix, uniting as it does the cortex of the gyrus fornicatus with the thalamus opticus.

Fig. 265.

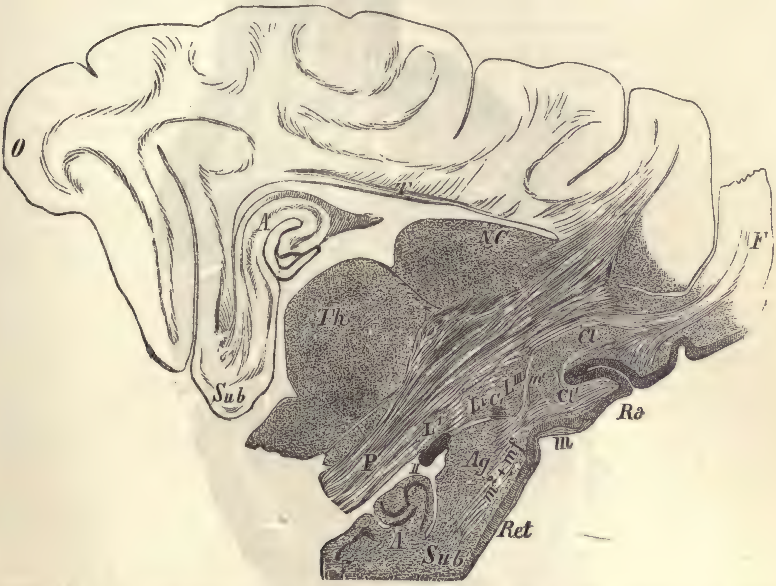

Fig. 265.* *Transparent profile section from the brain of a Dog, through the external olfactory convolution.* F, frontal extremity; O, occipital extremity of the cerebral lobe; T, section of the lowest bundles of the corpus callosum; *Sub A*, *Sub*, occipital and temporal portions of the ammon's horn. The convex piece connecting these two fragments is cut off at the external border of the caudex cerebri (and is, therefore, not included in this section); *Ra*, external olfactory convolution; m, superficial medullary substance of same (coming in reality from the bulbus); m^1, deeper laid medullary substance of the external olfactory convolution; *Cl*, claustrum; *LI*, *LII*, *LIII*, divisions of the nucleus lenticularis; *Ag*, nucleus amygdalæ; m^2+mf, point of union of the medullary substance of the olfactory convolution with that of the gyrus uncinatus; *Ret*, substantia reticularis, coalescing with the superficial medullary substance of the olfactory convolution; c, hemispheric portion of the anterior commissure; *II*, tractus opticus; *Nc*, nucleus caudatus;† *Th*, thalamus opticus; *P*, basis cruris cerebri.

Another striking example of this arched course taken by projection-system fibres is afforded by the stria cornea, which unites the extremity of the temporal lobe with the whole length of the inner border of the nucleus caudatus along which it curves.

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* L′ in the fig. is used twice by mistake. The one nearest to L‴ should be L″.—Translator.

† Corpus striatum and nucleus caudatus are in this treatise used synonymously, and the nucleus lenticularis is regarded as an independent ganglion, whereas, in many English works on anatomy, nucleus caudatus is used synonymously with nucleus intraventricularis corporis striati, and the nucleus lenticularis receives the name of nucleus extraventricularis corp. striat.—Translator.

The number of fibres in any given portion of the projection-system that passes from a certain region of the cortex into a ganglion, must necessarily

Fig. 266.

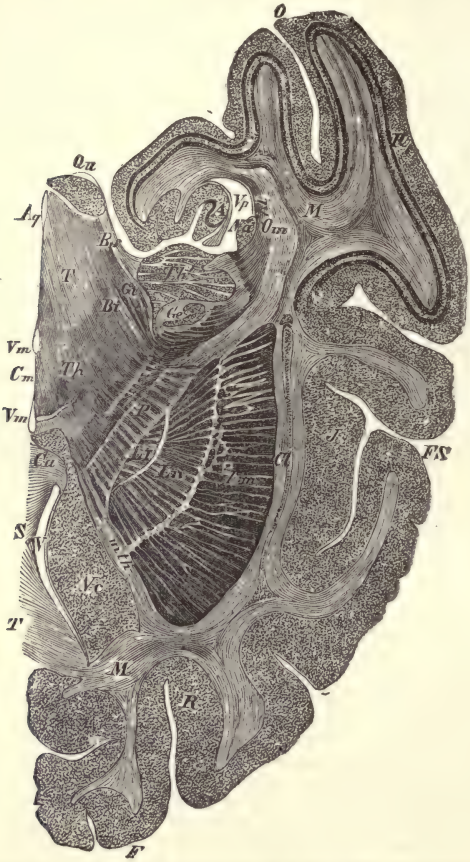

Fig. 266. *Horizontal section from the left half of the brain of Cercocebus cinomolgus.* *F*, frontal extremity; *O*, occipital extremity of the cerebral lobe; *FS*, entrance to the fissure of Sylvius; *I*, island of Reil; *Cl*, claustrum; *T*, corpus callosum; *S*, septum pellucidum; *Ca*, anterior commissure; *A*, ammon's horn; *V*, *Vp*, anterior and posterior horns of the lateral ventricle; *Vm*, third ventricle; *Cm*, middle (or soft) commissure; *Aq*, aqueductus Sylvii; *T'*, tapetum formed by the corpus callosum; *LI*, *LII*, *LIII*, the divisions of the nucleus lenticularis; *Nc*, *Na*, caput and cauda nuclei caudati; *Th*, that portion of the thalamus which is situated anteriorly to the corpora geniculata; *Th'*, tuberculum posterius (Polster) thalami optici; *Qu*, inferior corpus quadrigeminum (or bigeminum); *Gi*, internal corpus geniculatum; *Ge*, external corpus geniculatum; *m th*, bundles belonging to the corona radiata, passing from the frontal lobe to the thalamus; *P*, basis cruris cerebri; *Om*, tract of medullary substance from the occipital lobe, destined for the posterior tubercle (Polster or Pulvinar) of the thalamus, for the arm (brachium) (*Bs.*) of the superior corpus quadrig., for the two corpora geniculata; *Gi* and *Ge*, the arm of the inferior corp. quadrig., the basis cruris cerebri, and the nucleus lenticularis.

be in direct proportion to the size of the ganglionic mass which contains the cells in which they terminate. The two great anterior cerebral ganglia, the

nucleus caudatus, and the nucleus lenticularis, are so disposed that their largest ends, *the head of the nucleus caudatus* (*caput nuclei caudati*) and the *base* of the *wedge-shaped nucleus lenticularis*, look towards the *frontal extremity of the cerebral lobe.* While these ganglia are anteriorly so strongly developed, they dwindle in size posteriorly, the one to an insignificant tail-like extremity (Schweif d. Streifenhügels), the other to a thin jagged edge. It cannot then be doubted that the frontal lobe is represented in these ganglia, which are recognized to be associated with the motor functions of the body by a much larger number of projection-fibres than is the parietal lobe, and by a much larger number still than is either the occipital or the temporal lobe. On the other hand, certain portions of the *thalamus opticus*, and all the other masses of origin of the *tractus opticus*, receive a great number of fibres from the occipital lobe and the temporal lobe, and indeed these fibres constitute, for the masses of origin of the tractus (with exception of the thalamus), probably their only means of connection with the cerebrum. The relative sizes of the ganglia just mentioned, and the parts with which they are in connection, may be seen in fig. 266, where the *tuberculum posterius* of the *thalamus* (Sehhügelpolster) (*Th'*), *the external and internal corpus geniculatum* (Kniehöcker) (*Ge* and *Gi*), as well as the corpus quadrigeminum (*Qu*) with their projection-system fibres, are exposed to view in one horizontal section. One sees how, in the Ape, the fibrous rays passing from the occipital lobe into the ganglia of origin of the tractus opticus, gather themselves into a medullary layer of great thickness (*Om*) (optic rays, Sehstrahlungen, *Gratiolet*), which is enclosed by an abundant supply of fibræ arcuatæ. This layer is joined by a group of fibres which form the most posterior, and at the same time most exterior fasciculus of the basis cruris cerebri. Since now, as will be shown, this *most external bundle of the basis* passes over, at the time of the crossing of the pyramids into the *posterior column* of the spinal cord, it is plain that a representation of the posterior roots of the spinal nerves with which this bundle is united, is present within the same cerebral lobe which contains the optic rays alluded to. It has further been demonstrated by *Gratiolet* that those fibres of the projection-system which pass, not as he thought into the tractus opticus itself, but into the ganglia of origin of the same, arise, together with the fibres just mentioned which pass from the cortex into the outermost fascicle of the basis, by no means exclusively in the occipital lobe, but also in the temporal lobe of the cerebrum. Still another sensory surface (besides the skin and retina), viz., the Schneiderian membrane, sends an important representation to join this collection of nerve-fibres. It occurs as follows :

5. A large portion of the medullary substance of the olfactory lobe is to be seen in fig. 261, m^2c, stretching itself, as it were, towards the section of the *anterior commissure* which seems to turn to meet it, and traversing on its way the substance of the corpus striatum. This appearance is explained by the fact that these fibres follow an arch-shaped course in passing from the olfactory lobe to the anterior commissure, a small part of the convexity of which arch has been cut off, and left outside the section. At the same time it was known even to Burdach and Gratiolet, that the fibres of the anterior commissure run to the cortex of the *occipital* and *temporal lobes.* In these same regions of the hemispheres, then, three sensory surfaces are represented. 1, that supplied by the posterior roots of the spinal cord ; 2, the retina ; 3, the nasal surface ; and thus the occipital and temporal lobes stand as the counterpart of the frontal lobe, whose essential connections are with the motor ganglia. As far as that portion of the optic rays is concerned which enters the corpora geniculata, and also as regards the anterior commissure,

that fasciculus which forms the above-mentioned representation of the posterior columns of the spinal cord, the investigation of their connection with the cortex cerebri may be looked upon as closed.

The medullary tract which passes from the olfactory lobe into the anterior commissure contains, in Animals, a much larger number of fibres than do the rays which pass from the medullary substance of the hemisphere into this same commissure (fig. 261, *cm*², 265 *c*). In Man, on the contrary, the reverse is true; the anterior commissure is formed, almost exclusively, of fibres from the medullary substance of the hemispheres, while its connection with the olfactory lobes, corresponding to the slight degree of development of the latter, is but slight (fig. 264, *Ca M′R*).

In the anterior commissure, therefore, besides the fibrous bundles which cross from the olfactory lobe of one side to the hemisphere of the other, and which probably give rise to the rope-like, twisted appearance presented by the fasciculi in question, there must also, of necessity, exist true commissural fibres which unite on the one hand the two olfactory lobes, and on the other the two hemispheres. If the fibres that run from the olfactory lobe of either side to the corpus striatum of the same side be taken into consideration in this connection (Clarke, Walter, Gratiolet), we see that in the medullary substance of the olfactory lobe, the anterior commissure being reckoned as a part of this medullary substance, all the varieties of disposition of the fibres are represented which Johannes Müller describes as characterizing the chiasma nervorum opticorum. The analogy between the olfactory lobe and the retina is thus increased by the discovery of the existence of an olfactory-chiasma which is the analogue of the optic-chiasma.

Fig. 267.

Fig. 267. *Transparent cross-section from the upper ganglia of the caudex cerebri, and the island of Reil, passing through the anterior commissure (close behind the posterior border of the orbital convolutions and the olfactory lobe).* *I*, island of Reil; *Cl*, claustrum; *Ce*, external medullary capsule; *LIII*, third division of the nucleus lenticularis; *Nc*, caput nuclei caudati; *Nc′*, inferior (basal) portion of the head of the nucleus caudatus above the anterior perforated space; *M*, medullary substance of the cerebral lobe (pes coronæ radiatæ); *Ci*, internal capsule; *Ca*, middle connecting piece of the anterior commissure; *M′*, hemispheric portion of the anterior commissure; *R*, portion of the anterior commissure belonging to the olfactory lobe.

2. The Basis Cruris Cerebri and its Ganglia.

The superior member of the projection-system buries its peripheral extremity in a collection of ganglia which belong genetically, (1) to the original hemispheric vesicle, (2) to the original anterior and middle cerebral vesicles. Each of these ganglia has, morphologically speaking, two poles as it were, the one *central*, that which receives the superior member of the projection-system, the other *peripheral*, that from which the 2d member of the projection-system, the crus cerebri, emerges. The basis as well as the tegmentum cruris cerebri contains, besides the fibrous bundles destined to assist in forming the columns of the spinal cord, a large number of cerebellar fibres also, which part from the crus cerebri above the commencement of the spinal cord. Although the cerebral ganglia differ greatly one from another in conformation and structure, yet those connected with the basis and those connected with the tegmentum display so many points of resemblance, that the separation of them (for purposes of description) into these two classes, based upon their peripheral connections, suggests itself as a natural division. *The corpora geniculata* alone, not being directly connected with the crus cerebri, demand a separate consideration as appendages of the ganglia of the tegmentum.

The ganglia of origin of the basis cruris are, (1) *the nucleus caudatus*, (2) *the nucleus lenticularis*, (3) *the substantia nigra of Soemmering*, which lies between the basis and the tegmentum cruris cerebri.

The form of the nucleus caudatus (corpus striatum) is that of an arch, concentric with that formed by the entire hemisphere, and surrounding a transverse axis which forms a part of the caudex cerebri (Hirnstamm). This axis is the transversely disposed, wedge-shaped nucleus lenticularis, whose base is directed outwards, and whose point inwards. The relative position of the two ganglia, as so explained, is shown by fig. 266. The frontal branch of the arched corpus striatum, which lies in front of the nucleus lenticularis (*L*, *I*, *II*, *III*), is formed by the large head (caput) of the corpus striatum (*Nc*), its occipital portion by the insignificant tail-like extremity (*Na*). The transversely-disposed and the arch-shaped ganglia of origin of the basis cruris are, moreover, actually united together at the frontal end of the corpus striatum arch, through the fusion of the caput corp. striat. with the 3d member of the nucleus lenticularis (fig. 267, Nc^1, *L III*), and also at the temporal end of the same arch (fig. 256, *Cs*, *L*). The first-mentioned fusion will be more easily comprehended if it be remembered that the caput corp. striat., extending itself beyond that part of the latter which is visible in the lateral venticle, curves downwards to the base of the brain, where its inferior portion (Basaltheil) constitutes the gray matter which lies just above the *lamina perforata anterior* (fig. 261, *L*). Gratiolet gave to this inferior region the name of *olfactory district* (*Riechfeld*). I am able to bear witness to the justice of this designation by confirming the fact that this inferior district of the corp. striat. is invested by a thin layer of cortical substance, whose continuity with the cortex of the olfactory lobe may be easily demonstrated both as regards the neuroglia and the nerve-cell stratum of the latter. This stratum of cortical substance coalesces posteriorly with the gyrus uncinatus. Its presence shows the constancy of that law of development, in conformity with which the entire surface of the hemispheric vesicle becomes covered with cortical substance, and according to which, also, the septum pellucidum should properly be classed as a part of the cortex cerebri. The temporal end of the cauda

corp. striat. becomes fused, just behind the nucleus amygdalæ, with the temporal process which is sent off from the 3d member of the nucleus lenticularis (pedunculus nuclei lenticularis), as stated above. The substance of the caput corp. striat. is bent at one part of its inner surface into a gutter-like form and appears on the external (ventricular) surface of the septum pellucidum, where it occupies a space of about 8 mm. in height under the name of nucleus septi pellucidi (fig. 264, *J*).

Structurally considered, the corp. striat. contains the same delicate, punctated basement substance as does the cortex cerebri, and in it are scattered a few such bodies as are found in the corresponding part of the cortex and which look like free nuclei. The nerve-cells of the corpus striatum are in general of two sizes, viz., large cells with many processes, which attain a diameter of 30 μ, and small cells, only 15 μ in length, which are also multipolar, and which are found in much greater numbers than the large ones. It will probably be found that the nerve-cells of the one kind give rise to fibres of the spinal cord, and those of the other to cerebellar fibres. This opinion is justified by the following facts. It may be seen that the crus cerebri is at least three times as large as the pyramids of the medulla into which it passes. It can also be shown that this diminution in size is brought about within the limits of the pons Varolii, by the disappearance of certain of the fibres of the crus cerebri which turn from their course, and, with the aid of ganglion cells, enter the cerebellum by way of the processus cerebelli ad pontem (Brückenarme) (v. p. 657, same subject).

It is then evident that the ganglia of origin of the basis cruris give rise, at the same time, to fibres destined for the cerebellum. This fact furnishes a morphological argument for ascribing a motory significance to the cerebellum; for it cannot but be believed that the impulses communicated by the cortex to the corpus striatum and the similarly constructed nucleus lenticularis (which are recognized as motor ganglia), besides being transmitted to the spinal cord, call into play at the same time certain functions of the cerebellum.

The small cells mentioned, which are unquestionably nervous, should not be confounded with the elements which appear as free nuclei, and which Luys declared to be nerve elements standing in connection with the cerebellar fibres, and to have been carried along, as it were, by the fibres of the crus cerebri, into the gray substance of the corpus striatum. These chains of apparently free nuclei, which are stretched parallel to the nerve fibres, are in fact simply the cell-elements of the connective-tissue reticulum of the medullary substance in general, where they are of universal occurrence.

The *first member of the projection-system* enters the corpus striatum under four different forms:

1st. As fibres belonging to the corona radiata, coming from the hemispheric arch throughout its entire length.

2d. Under the form of a bundle of fibres, the stria cornea, which runs from the cortical substance of the temporal extremity to the most anterior part of the caput corp. striat., following an arch-shaped course along the inner border of the latter ganglion.

3d. Under the form of fibres which connect the cortical substance of the olfactory lobe with the corpus striatum, whether it be the superficial fibres which take their rise in the bulbus, or the deeper laid medullary substance of the olfactory lobe (fig. 261 m^1). That portion of the olfactory medullary substance that enters the anterior commissure, seems merely to traverse, without interruption, the substance of the corp. striat. The medullary fibres

of the olfactory lobe also pass, in arching lines, through the nucleus septi pellucidi.

4th. Under the form of the pedunculus septi lucidi which unites the cortical substance of the septum with the inferior region of the corp. striat.

This inferior region of the caput corp. striat. is, from just above the lamina perforata anterior to the neighborhood of the anterior commissure, made of a structure unlike that of the rest of the corp. striat. This structure has not yet been described with monographic accuracy, but two of its most striking peculiarities are, 1st, that it contains nerve-cells of rather small size, agglomerated together so as to form circumscribed piles of nuclei-like elements; 2d, that it contains a kind of element which is not to be found in any other part of the collective cerebral ganglia, viz., very small granules (Körner) (6 μ in diam.) which, disposed in closely packed masses, establish a point of structural relationship between the region under consideration and the olfactory lobe, by the medullary fibres of which it is traversed. To judge from its formation, peculiar both in respect to the form and to the arrangement of the elements, we should infer that an independent function should be ascribed to this mass of gray substance, although it appears to form an inseparable part of the corpus striatum.

The manner in which the *corpus striatum* gives rise to its contingent of the *crus cerebri* is very simple, for the fibres which go to form the latter converge like radii from the concavity of the arch made by the former toward the base of the brain, and unite in the basis cruris cerebri (fig. 261 *P*).

In general terms (the stria cornea being left out of consideration) the *outer*, which is at the same time the *upper* border of the corpus striatum, represents its central pole,—that which receives the fibres of the corona radiata; while the *inner* or *lower* border represents its peripheric pole,—that from which the fibres of the crus cerebri emerge.

The crural fibres of the corpus striatum traverse in their course the upper layers of the inner capsule (capsula interna) (fig. 267, 268 *Ci*), to reach its lower layers. This broad medullary tract, the inner capsule, the two parts of which, as they appear in a horizontal section, seem to unite at an obtuse angle, separates anteriorly the corpus striatum from the nucleus lenticularis, posteriorly the latter from the thalamus opticus. The upper half of its layers is made up of the 1st member of the projection-system, the lower extremity of the respective section of the corona radiata (pes coronæ radiatæ), the lower half of the same by the 2d member of the projection-system, viz., the basis cruris cerebri. The extremity of the corona radiata is however, as it lies in the inner capsule, overarched by the corpus striatum, and is therefore interwoven with the crural fibres of the latter, which cross the direction of its own, as fig. 261 illustrates. The fibres of the corona radiata represented in the figure (*Th*), run from the frontal lobe into the thalamus opticus.

The course of certain fibrous bundles, coming from the corpus striatum within the crus cerebri itself, is somewhat complicated. That is to say, after removal of the tractus opticus, certain bundles are to be seen running transversely and parallel to the tractus, which emerge from among the external fasciculi of the crus cerebri, and disappear again among its internal fasciculi. These bundles are made up of fibres which have come from the cauda corp. striat., which is situated rather externally to the rest of the ganglion. Their downward course to the spinal cord lies in the inner portion of the crus, and to reach this position they are obliged thus to pass superficially across the intermediate fasciculi. They are to be carefully distinguished from the ansa

peduncularis (Hirnschenkelschlinge), which latter, when it is in contact with the crus at all, is never entwined with the fibres on two sides of it.

The *nucleus lenticularis* (figs. 256, 265, 266, 267, 268), the second ganglion of origin of the basis cruris, is of precisely the same histological structure with the intraventricular portion of the corpus striatum. It contains the two varieties of nerve-cells, differing in point of size, but there is in it no district of peculiar structure analogous to that district of the inferior portion of the corpus striatum which is traversed by the medullary fibres from the olfactory lobe. The shape of this ganglion is that of a wedge. The base of the wedge is directed towards the frontal lobe and the island of Reil, its point passes over into the basis cruris, and posteriorly it terminates in a thin, jagged, saw-like edge. On cross-sections of this ganglion its nerve-fibres appear disposed in two general directions, viz., in lines radiating from the point of the wedge towards its base, and in layers concentric with the curved base of the wedge, the component fibres of which layers

Fig. 268.

Fig. 268. *Transparent cross-section passing through the region of the island of Reil and the ganglia of the caudex* (*Stammganglien*). Human brain. (Slightly magnified.) JJ^1, cortical and medullary substance of the island of Reil; *Cl*, claustrum. Near its base are some of the transition masses which connect the claustrum with the nucleus amygdalæ; *V*, gray substance lining the 3d ventricle; $L,^1$ $L,^2$ $L,^3$ the nucleus lenticularis; *Nc*, nucleus caudatus; *B*, inferior region (Basaltheil) of the nucleus caudatus; *VC*, anterior commissure; *IK*, region of the inner, *aK*, region of the superior stalk (Stiel) of the thalamus opticus; *M*, pes coronæ radiatæ; *Ce*, capsula externa; *Ci*, capsula interna; *Schl*, *L*, *St*, *Z*, the four layers of the substantia innominata or crural sling (Hirnschenkelschlinge); *G*, the anterior descending pillar of the fornix; *A*, commissure in the central tubular gray matter; *II*, nervus opticus, together with the inferior optic ganglion which lies above it.

run downwards from the inner capsule toward the base of the brain (figs. 265, 266, 268). These latter fibres form the concentric partitions, the *laminæ medullares*, which divide the nucleus lenticularis into its three so-called members (Glieder), the innermost of which is intimately connected

with the origin of the crus cerebri, while the outermost is separated only by the thin medullary layer of the outer capsule from the claustrum, which has been shown to belong morphologically to the cortical substance of the island of Reil (figs. 267, 268 *Ce*), also (figs. 265, 266). This external capsule is not connected by nerve-fibres with the surface of the nucleus lenticularis on which it lies, but the two are united together by means of loose connective tissue. A few slender and seemingly inconstant nerve-fibres, which penetrate the surface of the ganglion, form an exception to the general rule.

The two inner divisions of the nucleus lenticularis are distinguished from the much larger third division by their great richness in medullated fibres, which gives them the name of *globus pallidus*. This is due to the fact that the third division, while containing, in virtue of its position at the base of the wedge, more gray substance than does either of the others, is traversed only by as many fibres as arise within its own limits, while the inner divisions are traversed by fibres coming from the third division and bound for the basis cruris, as well as by their own. Just as the corpus striatum stretches its slender posterior extremity forward to the point of the temporal lobe, so also the nucleus lenticularis thrusts its temporal process (pedunculus nuclei lenticularis), which is of inconsiderable size in comparison with its frontal portion, toward the same lobe to receive its medullary rays.

The upper border (as it appears in cross-sections) (fig. 268) of the nucleus lenticularis represents its central pole, where the fibres of the corona radiata, leaving the inner capsule, penetrate into the ganglion substance. That which appears in cross-sections as the lower border of the nucl. lentic., and its inner extremity, represents the peripheral pole of the ganglion, from which a large part of the fibres of the basis cruris proceed. It is evident from the form of the nucleus lenticularis, that its contingent of fibres received from the cortex of the frontal and parietal lobes must be incomparably greater than that from the occipital and temporal lobes. Apart from the quantitative distribution of the fibres, however, the lenticular nucleus must be regarded as standing in connection with all parts of the cortex cerebri. The walls of the fissure of Sylvius also, *i. e.*, the island of Reil and the surrounding parts, send their projection-system fibres into this ganglion. These fibres from the island of Reil run, however, by no means in straight lines into the convex surface of the third division of the ganglion, which lies so nearly in apposition to the island, but they follow rather a curving course, running, while in the medullary substance of the island, parallel to the convex surface of the lenticular nucleus, then passing over the edge of the same into the inner capsule, and, as the outermost fasciculi of the latter, entering finally into the ganglion. The fibres of the 1st and 2d members of the projection-system which traverse the nucleus lenticularis (considering them for the moment as forming one continuous system, unbroken by the intervention of ganglion cells), take by no means the shortest and most direct path through the ganglion, but, on the contrary, describe complicated spiral lines, made up of descending portions, which are concentric with the convex surface of the ganglion and radiating portions which are directed inwards (*i. e.*, towards the crus cerebri). All the radiating, middle, and lower fibrous bundles in the third division of the nucleus lentic., for instance, entered the ganglion more anteriorly at its upper border and descended parallel with its convex outer surface before they assumed their direct course toward the basis cruris. The bundles of fibres become aggregated together toward the interior in constantly increasing numbers, in proportion, of course, to the length of time that the line (as seen in cross-sections) which represents the

receiving surface or pole of the ganglion has been in contact with the cerebral medullary substance, the outer end of this line being regarded as its functional zero-point, as it were. Thus aggregated together, these fibrous bundles, whose concentric paths were, in the 3d division of the ganglion, only to be traced by the microscope, appear as defined, plainly visible lines, the *medullary partitions* (laminæ medullares) between the *divisions* of the ganglion, which partitions, since they also contain nerve-cells and are intersected by other bundles running in radiating lines, become intricate ganglionic networks.

The number of the large nerve-cells in these fibrous partitions is very considerable, and they are plainly disposed with their long axes pointing in the direction of the course of the concentric bundles. In the globus pallidus of the ganglion the nerve-cells are closely packed, and the interstitial, amorphous, connectile substance is but poorly represented. A certain proportion of the fibres of which the laminæ medullares are composed do not, in their further course, traverse both or even one of the inner divisions of the lenticular nucleus, but run along the inferior surface of the ganglion directly into that part of the inner capsule which belongs to the crus cerebri. On the surface, obtained by cross-section, of the crus cerebri, the latter fibres occupy its innermost segment, in order to reach which position they not only pass the lower surface of their parent ganglion, but also cross transversely the external and central fasciculi of the crus cerebri in the form of a sort of sling, which is pretty nearly parallel with the tractus opticus, and is designated as the sling of the lenticular nucleus (Linsenkern-Schlinge). (Fig. 268 and 270 *Schl.*). This so-called sling forms the lowest stratum of the ansa peduncularis of Gratiolet, described p. 691, or of the substantia innominata of Reil. The haste shown by these fibres, coming as they do from the most externally disposed ganglia, to reach their interior position at the expense of crossing the other fibres, is probably to be accounted for by their being destined to arrive very early at their place for crossing the median line.

These innermost fasciculi of the basis cruris cerebri terminate peripherally in the central tubular gray matter, as high as at the region of the corpus quadrigeminum superius, where they enter the nuclei of origin of the nervus oculo-motorius and the nervus trochlearis, after first crossing the median line, just as the anterior pyramids do later in passing into the lateral columns of the spinal cord. It appears indeed quite probable that this ansa lenticularis contains within itself the fibres, by means of which the nucleus lenticularis is brought into connection with the collective *motor nerves of the cerebrum.*

In cross-sections which (fig. 271) pass through the posterior end of the third ventricle the formation of the basis cruris appears completed, not only as regards that part of its fibres which are derived from the nucleus caudatus and nucleus lenticularis, but also in respect to the fibres derived from the cortical substance of the occipital and temporal lobes, which form the most external fasciculus of the basis cruris. This group of fibres is, at its entrance into the crus, covered over by the posterior tubercle of the thalamus and by the corpora geniculata, and in cross-sections, therefore, is to be seen just in advance of these ganglionic masses (fig. 266). While descending through the region of the mid-brain (corp. quad.), the basis cruris receives, however, a contribution from the third of its ganglia of origin, the gray substance of Soemmering (locus niger, substantia nigra) (fig. 271, 272 *S*). This broad, thin mass of ganglionic substance lies like a partition between the basis and the tegmentum cruris cerebri. It

stands in connection centrally with a thin, fan-shaped layer of fibres belonging to the corona radiata which terminate in it, while peripherally (fig. 271) it sends out fibrous bundles which appear on the transversely cut surface of the crus cerebri in the form of a well-defined network, which cuts up the inner and central part of the section into minute divisions. This network encloses straggling elements belonging to the system of large pigmented cells, to which the ganglion owes its name of substantia nigra, and besides them a number of very small cells. The external division of the basis cruris, that which is derived directly from the cortex cerebri, remains free from admixture with the fibres of the substantia nigra of Soemmering. The basis cruris cerebri has then four different regions of origin. They are: 1. *The cortical substance of the occipital and temporal lobes.* 2. *The nucleus caudatus.* 3. *The nucleus lenticularis.* 4. *The substantia nigra.* The fibres furnished by these ganglia are so distributed that the most external region of the basis is made up of fibres derived directly from the cortex cerebri, the innermost region unquestionably of fibres furnished by the nucleus lenticularis (sling of the nucleus lenticularis) and the intermediate region, the largest of all, of fibres from the nucleus caudatus and the nucleus lenticularis in common. The fibres from the substantia nigra of Soemmering are distributed among those from the other ganglia over the inner and central regions of the basis cruris.

The dimensions of the cerebral lobes, and those of the basis cruris with its ganglia of origin, whether they increase or diminish, maintain the same relative proportions in Mammal brains. For instance, the weight of the cerebral lobes in Man, in the harlequin Ape, or in the Deer, being respectively 78%, 70.8%, and 62% of the weight of the entire brain, so the weight of the lobus caudicis (Stammlappen=Island of Reil, together with nucleus caudatus and nucleus lenticularis) of the same animals is respectively 58%, 40%, and 33.3% of the weight of the entire caudex cerebri (Hirnstamm), and further the height of the basis cruris is to that of the tegmentum cruris in the following ratio: in Man, of 1 : 1; in the Ape, of 1 : 3; in the Deer, of 1 : 5. This relative increase in size of the ganglia of the caudex in Man affects the nucleus lenticularis far more than the nucleus caudatus, which is probably due to the fact that the development of the latter is dependent upon that of a region of the brain which in Man is but poorly represented, viz., the olfactory lobe.

3. The Tegmentum Cruris Cerebri with its Ganglia.

The ganglia belonging to the posterior division of the crus cerebri are, as is shown by a comparison of the size of the two in different animals, functionally independent of the cerebral lobes, and are but poorly developed in the Human brain as compared with that of the lower animals. For example, the weight of the thalami optici in Man constitutes but 19% of that of the entire caudex cerebri, while in the Ape it constitutes 22.9%, and in the Deer 30% of the same. On the other hand, the weight of the corpus quadrigeminum constitutes in Man 6.5%, in the Ape 10%, and in the Deer 16% of that division of the encephalon.

The principal ganglia of origin of the tegmentum are: 1. *The thalamus opticus.* 2. *The corpus quadrigeminum.* These ganglia have in common, besides their connection with the spinal cord, a connection with the tractus opticus also. This latter connection they share with the *corpora geniculata*, which may therefore be fairly regarded as an appendage to these ganglia. The tegmentum, moreover, receives fibres from: 3. *The corpus mammillare;* 4. A ganglion embedded in the *crural sling* (ansa peduncularis, Hirnschenkelschlinge); 5. The pineal gland (conarium).

The *thalamus opticus*, distinguished by the color of its belt of white fibres,

the stratum zonale, from the gray surface of the nucleus caudatus, seems at the first glance to present its own gray ganglionic substance, exposed and uncovered, at that part of its surface which appears in the third ventricle. This ventricular gray substance forms in reality a layer foreign to the thalamus itself, and, together with the neighboring tuber cinereum, with which it is continuous, with the infundibulum and the posterior part of the hypophysis cerebri, belongs to the central tubular gray matter. This posterior part of the hypophysis in which the tubular gray matter ends is described by Luschke as having, like the inferior extremity of the same gray matter in the region of the filum terminale, very few of the characteristics of nervous tissue, but rather those of connective tissue. The anterior part of the hypophysis is certainly not to be ranked as belonging to the nervous system, but as a foreign, simply contiguous formation. It contains a stroma of connective tissue which encloses vesicular bodies filled with cells of 30–90μ in length, and is classed by Ecker among the vascular glands, by Henle as a formation similar to the medullary substance of the supra-renal capsules.

The central tubular gray matter lining the *third ventricle* has not yet been described with monographic accuracy. At present the following formations alone have been distinctly traced:—

1. At the lateral border of the tuber cinereum lies the *inferior optic ganglion*, which is 1.5mm. broad, and contains spindle-shaped cells 30μ in length and 15μ in breadth. It begins just above the optic commissure, and stretches along immediately over the tractus opticus as far as the posterior border of the tuber cinereum, a distance of more than a centimetre. I regard, with Luys, this optic ganglion as a part of the tuber cinereum, because it projects downwards, in company with the latter, into the lamina cinerea, beyond the surface of the lamina perforata anterior, of which J. Wagner considers it to be a part, and because it extends farther backward than the latter. Like the tractus itself, however, it certainly follows the inner border of the anterior perf. space. On profile sections (Fig. 270 *II'*) this ganglion has a sickle-like shape, the concavity looking forward. According to Luys, the two ganglia touch at the median line, a fact which I have not been able to verify, and he describes the roots of the optic nerve, which have their origin in them, as crossing the median line even within the tuber cinereum, which is certainly a mistake, for the delicate bundles of fibres (which, contrary to Foville's opinion, are surrounded by medullary sheaths) take, as soon as they reach a position just over the chiasma, an outward course to enter the optic nerve. The strongest argument for the existence of uncrossed fibres in the optic nerve is therefore afforded by the course of the fibres in question, as here described. Appreciating as I do the difficulty of deciding such a question by means of section preparations, I do not feel justified, as regards the remainder of the optic nerve, either in denying or confirming, from personal observation, Biesiadecki's assertion that all its fibres decussate in the chiasma with those of the opposite side.

The fact that the opticus stands in connection with the central tubular gray substance, by no means justifies us in classing this so-called nerve with the peripheral nerves that spring from this same gray matter. The analogy between the optic chiasma and the olfactory chiasma, the retina and the bulbus olfactorius, as well as the resemblance which the optic fibres, in virtue of their fineness and the absence of a fibrous sheath, bear to the fibres of the central medullary substance, render it improbable that the optic nerve belongs to the peripheral part of the projection-system. It is more probable that the root of which we have been speaking should be regarded as a part of the superior member of the projection-system, the concentric layers of

gray matter of the retina, which are analogous to those of the cortex cerebri, acting as its central extremity, *the inferior optic ganglion* as its peripheral extremity, in which case certain as yet undiscovered nerve tracts must be supposed to pass, by way of the central tubular gray matter, to some organ of the periphery, perhaps to the muscles of the eye.

2. Immediately behind the inferior optic ganglion lies, enclosed within the tuber cinereum, a certain commissure (fig. 268, *A*) whose fibres turn backwards within the central tubular gray matter, their termination being as yet unknown.

3. Without entering into connection with the substance of the thalamus, there runs along the central tubular gray matter, at first of the third ventricle, later of the aqueductus and fourth ventricle, the *posterior longitudinal fasciculus* of the tegmentum cruris cerebri (figs. 268 to 276, *L*). This fasciculus terminates centrally in a broad thin ganglion (fig. 268, *L*), which lies beneath the ansa lenticularis, and constitutes the second stratum of the mass called by Reil substantia innominata, by Gratiolet anse pedonculaire, which passes transversely across the basis cruris above the tractus opticus (fig. 268, *Schl*, *Z*). The cells of this ganglion extend into the external capsule whose component fibres (except in so far as they belong to the association system), coming from the cortex of the operculum (Klappdeckel) and passing over the surface of the nucleus lenticularis without penetrating into it, converge regularly and terminate in this ganglion of the *ansa peduncularis.* Scattered bundles of fibres, with and without spindle-shaped cells, about 50μ long and 15μ broad, which lie inserted in their course, traverse in this process the superficial layers of the third division of the nucleus lenticularis. Besides the operculum, the other parts of the walls of the fossa Sylvii send fibres to this ganglion, and part of them come from the cortex of the island of Reil and from the temporal lobe, traversing the claustrum on their way. The posterior longitudinal fasciculus receives further fibrillæ from the lowest part of the infundibulum. These latter fibres run across the inner side of the anterior pillars of the fornix, while the great mass of the posterior longitudinal fasciculus lies to the outside of these pillars.

4. The descending branch of the anterior pillar of the fornix also lies in the central tubular gray matter, as well as the first part of the ascending branch, before it penetrates the substance of the thalamus opticus (fig. 269, *Fd*, *Fa*).

According to Meckel, Arnold, Jung, and Luys, the descending branch of the crus fornicis becomes fused, before its entrance into this gray matter, with the anterior extremity (but surely not with the whole length!) of the stria cornea, and the habenula conarii (Zirbelstiel). Together with the crura fornicis, the upper half of the spherical *corpus candicans* (fig. 269, *M*) becomes embedded in the inferior part of the central tubular gray matter.

The corpus candicans (s. mammillare) is a ganglion, which lies in a loop made by the anterior pillar of the fornix in twisting back upon itself (to enter the thalamus), and by its means a certain number of the fibres of the fornix are made to pass directly into the tegmentum cruris cerebri. It is a mistake to suppose, with Jung, that the fibres from the fornix simply traverse the substance of the corpus candicans, and that the superficial nerve-fibres which enclose the latter are to be referred to a different source. On the contrary, the descending branch of the crus fornicis first invests the outer and posterior surfaces of the ganglion, and then, twisting on itself, invests, under the form of the ascending branch of the same crus, the inner and anterior surfaces.

In the course of this process, a portion of the fibres of the fornix traverse the substance of the ganglion, which contains spindle-shaped cells, 20 to 30 μ by 9 μ, and from the upper border of which (fig. 269, *m*) issues the fasciculus destined for the tegmentum cruris. The greater part of the fibres of the crus fornicis, however, simply curve round the outside of the ganglion, enclosing in their course, especially in the ascending branch of the crus fornicis, nerve-cells, 30 to 45 μ by 15 μ, which lie strictly parallel to the fibres, and which appear to coincide, in point of size, with the terminal cells of this same ascending branch, which are found in the anterior tubercle of the thalamus (fig. 270, *G*, *Ta*). The fibres of the fornix, then, terminate at their peripheral extremity in cells of two kinds, of which the smaller are found in the corpus mammillare, the larger in the tuberculum anterius thalami optici.

An entirely false idea is formed of the *shape of the thalamus opticus* if the superficial gray matter, of which we have just been treating, be regarded as making a part of the ganglion. In that case it would appear as if the anterior extremity of the thalamus reached to the very base of the brain, whereas, in fact, this extremity is farther removed from the base of the brain than any other part of the ganglion; for the anterior extremity, which is the thinnest part of the thalamus, lies not only above the crus cerebri, but also above a part of the wedge-shaped nucleus lenticularis, as is seen in cross-sections (fig. 268, *aK*, *L*, *I*, *II*, *III*). Even Burdach's illustration, which compares them to "two knobs resting upon the crura cerebri," conveys no correct impression of their shape. The form of the thalamus, subject, of course, to irregularity in the distribution of the parts, is essentially that of an arch surrounding a transverse axis, which was the underlying form of the cerebral lobes also, and, among the ganglia, of the corpus striatum. Just as the nucleus lenticularis served as an axis for the corpus striatum, so, for the arch made by the thalamus, that place is taken by certain transversely laid ganglia, or rather in part by the ganglia themselves, in part by the nerve-tracts that run transversely from them into the medullary substance of the cerebrum. These axes, round which the thalamus arches, are the brachia corp. quadrigem. (fig. 266, *Q*, *Bs*), together with the *internal* corp. geniculat., which stands in close relation to the brachium corp. bigem. infer. (fig. 266, *Gi*). That part of the thalamus which lies anteriorly to the axis of the arch (fig. 266, *Th*) is much the longer portion of the ganglion; that which lies posteriorly (the posterior tubercle, das Pulvinar) (fig. 266, *P*) is by far the shorter.

At the region of the tuberculum posterius, the breadth of the thalamus is greater than at any other part; just in front of the axis comes its greatest thickness, and at its anterior extremity both dimensions are less than anywhere else.

Such being the general form of the thalamus, it is proper only under certain limitations to recognize the existence of special nuclei of gray substance within its limits; for, strictly speaking, the gray matter of the thalamus forms but a single mass, nor have any striking differences in the texture of its different parts disclosed themselves to us as yet. The more or less complete separation of the substance of the thalamus into different nuclei, is due on the one hand to the *manner of entrance* of the fibres of the first member of the projection-system, and on the other to the *mode of origin* of the fibres of the *crus cerebri within the ganglion*, and the study of these two points will make clear to us the position of the supposed special nuclei.

The *superior member of the projection-system* then, coming from the frontal lobe, from the walls of the fossa Sylvii, and from the temporal lobe,

penetrates in fourfold manner into the anterior extremity of the thalamus. In three directions blunt processes, so to speak, project from the substance of the thalamus to meet the fibres from the corona radiata, and unite with the compact masses of medullary substance as if with pedicles.

1. The *anterior pedicle* of the thalamus penetrates from the frontal lobe, between the corpus striatum and the nucleus lenticularis, directly into the anterior extremity of the ganglion, taking part, on its way, in the formation of the internal capsule of the nucleus lenticularis (figs. 266, 261, *mth*). Once within the substance of the thalamus, this compact group of fibres splits into a cone of diverging rays, in consequence of which the anterior part of the thalamus appears on longitudinal sections under the form of a blunted cone (fig. 261). The most superficial portion of this pencil of rays helps to form the stratum zonale before it penetrates into the substance of the ganglion proper. 2. The *inferior pedicle* of the anterior tubercle of the thalamus enters from the substantia innominata, splits up in like manner into a pencil of radiating fibres (figs. 268, 270, *St*, *aK*, *IK*), and some of its bundles, especially in the inner division of the thalamus, may be traced a long distance backwards. This pedicle forms at its origin the third stratum of the ansa peduncularis (fig. 268). Its fibres spring from the cortex of the fossa Sylvii, and from that of the temporal lobe. 3. This third stratum of the ansa peduncularis is succeeded by a fourth, which also penetrates, but by a more indirect route, the substance of the thalamus, viz., by joining itself to the component fasciculi of the *stratum zonale* (fig. 268, *Z*), which pass in spiral curves over the surface of the ganglion preparatory to entering the superficial layers of its gray matter. The *substantia innominata of Reil* admits, then, of division into four layers, each of which takes a different course: 1, the ansa peduncularis (Linsenkernschlinge), destined to join the basis cruris; 2, the ganglion of the ansa peduncularis with the fibres of origin of the posterior longitudinal fasciculus to which it gives rise; 3, the inferior pedicle of the thalamus opticus; 4, the fibres destined for the anterior temporal portion of the stratum zonale. The course of each of these sets of fibres composing the ansa peduncularis may be divided into two portions. During the more central portion of their course the fibres generally run in a direction parallel to that of the tractus opticus (fig. 268) and appear on frontal cross-sections as longitudinal lines, while during the more peripheric portion of their course they become visible in longitudinal sections, no longer parallel with each other, but beginning to diverge toward their various terminal destinations. 4. The fourth mode in which the fibres of the first member of the projection-system enter the anterior part of the thalamus is that adopted by the ascending branch of the crus fornicis, which represents the cortex of the gyrus fornicatus and forms the superior pedicle of the thalamus (fig. 270, *G*). After making an S-shaped curve, in order first to pass to the inside of the posterior longitud. fasciculus, and then to reach a somewhat external part of the thalamus, this ascending crus fornicis passes directly forwards and upwards, and, forking into two parts, as may be readily seen on cross-sections, it spreads out its fibres in the *superior nucleus of the thalamus*, whose anterior extremity gives rise to the protuberance on the surface of the ganglion called the tuberculum, or genu anterius (fig. 270, *Ta*). The tuberculum anterius forms, however, only the head (caput) of a sort of nucleus caudatus of the thalamus, of which the remainder is represented by the rest of the above-mentioned superior nucleus, which is prolonged backwards and outwards, terminating in a caudal extremity which disappears in the pulvinar (tuberculum posterius). This mass, although by no means completely separated from the surrounding ganglionic substance,

is the best defined special nucleus of the thalamus, for the stratum zonale splits into two layers, which embrace it as it were, making its boundary-lines easily recognizable both on longitudinal and on cross-sections. The anterior portion of this gray nucleus certainly coalesces with the substance of the rest of the ganglion, and is not to be distinguished from it.

Fig. 269.

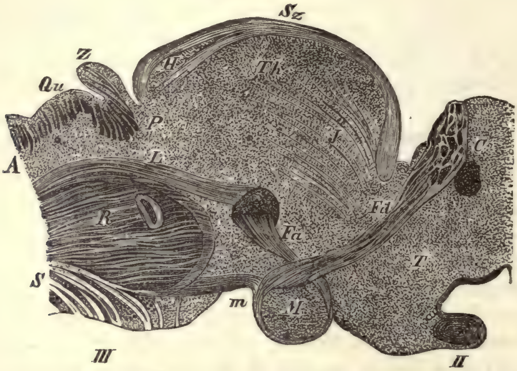

Fig. 269. *Transparent profile section passing through the Human thalamus opticus near its inner surface.* *Th*, Thalamus opticus *Q*; *u*, Corpus quadrigeminum; *Z*, Conarium; *H*, The ganglion mammillare; *T*, Tuber cinereum; *R*, Centrum rubrum of the tegmentum (rother Kern d. Haube); *S*, substantia nigra; *A* marks the neighborhood of the aqueductus Sylvii; *II*, chiasma nerv. opt.; *C*, commissura mollis; *III*, nervus oculo-motorius; *Sz*, stratum zonale; *J*, fibres traversing the inner division of the thalamus, coming from its inferior pedicle; *Fd*, descending branch of the crus fornicis; *Fa*, ascending branch of same; *P*, commissura posterior; *L*, posterior longitudinal fasciculus; *M*, fibres passing from the corpus mammillare to the tegmentum cruris cer.

The internal capsule of the lenticular nucleus contains fibres destined not only for the anterior extremity, but also for the body of the thalamus opticus, which have their origin in the *posterior part of the frontal lobe*, and in the *temporal lobe*. The surfaces of the thalamus and of the nucleus lenticularis, taken together as they appear in cross-sections (fig. 268), represent roughly the two halves of a square, of which the diagonal is formed by the *internal capsule* by which the two ganglia are separated (fig. 268). While, as we have seen, the upper surface (in cross-sections the upper border) of the lenticular nucleus formed its central receiving region or pole, the analogous region of the thalamus is formed by its lower surface, which is inclined obliquely downwards and inwards, for it is this surface which is in contact and connection with the inner capsule.

It should scarcely be presumed, however, that the central part of the thalamus is exclusively in connection with the parietal lobe in whose immediate neighborhood it lies. Apart from the fact that the fibres of the *anterior pedicle* of the *thalamus* from the frontal lobe, and those of the *inferior pedicle* from the temporal lobe, may be traced backwards for some distance, it may be shown that the temporal lobe also sends out fibres that traverse for a considerable distance the superficial regions of the gray matter of the thalamus. These latter fibres, arching upwards from the temporal lobe, enter the thalamus from behind, and in so doing they cross the fibres from the corona radiata which have a direct course (from the parietal lobe for instance), and form with them a fibrous web, the lattice-like stratum

(Gitterschichte) of the thalamus. This interlacement takes place, not in the cerebral medullary substance, but just within the limits of the thalamus itself, so that a thin layer of the substance of the latter lies, forming as it were a claustrum for the thalamus opticus, imperfectly separated from the rest of the ganglion by the open-work capsule of nerve-fibres that form its lattice-stratum, or rather lies enclosed in the meshes of the latter (fig. 266,

Fig. 270.

Fig. 270. *Transparent profile section through the anterior tubercle of the Human thalamus opticus.* *Ta*, tuberculum anterius; *JK*, inner division of the thalamus; *K*, corp. quadrigem.; *W*, neighborhood of the aqueductus Sylvii; *RK*, red centre or nucleus of the tegmentum; *SS*, substantia nigra of Soemmering; *F*, basis cruris cerebri; *II*, tractus opticus; *II'*, inferior optic ganglion; *Zi*, stratum zonale; *cc*, anterior commissure; *Ch*, posterior commissure bending downwards to join the tegmentum; *G*, ascending branch of the crus fornicis; *JK*, *L*, *Schl*, three converging fasciculi that by their convergence form the ansa peduncularis; *JK*, being the inferior pedicle of the thalamus; *L*, the posterior longitudinal fasciculus; *Schl*, the ansa lenticularis.

betw. *Th*, and *P*). The merit of having first demonstrated on section-preparation the radiation from the inner capsule into the thalamus opticus belongs to Kölliker, whose histological description of the structure of the brain, in his Microscopic Anatomy, shows altogether a rare comprehension not only of the gross anatomy of the organ, but also of the minute details of its structure.

In the posterior regions of that part of the thalamus which is still exposed in the third ventricle, *i. e.*, the part anterior to the posterior tubercle, the ganglion is in direct contact with the cerebral medullary substance proper, since at this region the inner capsule is no longer present, its limits being the same with those of the nucleus lenticularis, which does not extend so far posteriorly. In this region the thalamus may be separated into an upper and a lower division, marked off from each other by a process of medullary substance that projects between them (fig. 271, close to *IIR*). The gray sub-

stance of the upper and of the lower division of the thalamus coalesce completely, and the two are traversed conjointly (fig. 271, *Th*) as far as the innermost of the laminæ medullares (T''), of which we shall speak again below, by exactly similar radiating fasciculi that are arranged in layers, which alternate with layers of gray substance of about equal thickness, in which the fibres terminate. The nerve-cells of the thalamus are on an average 30 μ long, by 10 μ broad, spindle-shaped, and disposed with striking regularity parallel to the radiating fibres just referred to. Those of the *superior* and those of the *inferior* division seem to be of the same size. These radiating fibres, which are all apparently of the same nature, and which terminate thus in the conjoined *superior* and *inferior* divisions of the

Fig. 271.

Fig. 271. *Transparent cross-section from Human thalamus opticus and crus cerebri at the posterior border of the 3d ventricle.* *M*, cerebral medullary substance; *Th*, thalamus opticus; V_3, 3d ventricle lined by the central tubular gray matter of the inner surface of the thalamus; *H*, ganglion habenulæ; *Cm*, the centrum medianum of Luys; *C*, corpus geniculatum externum; *Nc*, nucleus caudatus; *T T*, tegmentum cruris cerebri; *R K*, centrum rubrum of the tegmentum, into which bundles of fibres are seen between *II*, *R*, and *S* to pass from the cerebral medullary substance; *P*, basis cruris cerebri; *S*, the substantia nigra; *II*, tractus opticus; *Sz*, stratum zonale; *R*, the fibres of the superior division of the thalamus from the medullary substance of the cerebral lobes; *II R*, the radiating fibres in the thalamus, which pass from the tractus opticus into its inferior division; T', the concentric laminæ medullares, made up of fibres destined for the tegmentum; *L*, posterior longitudinal fasciculus cut across transversely.

thalamus, have nevertheless two distinct centres of origin. Those of the superior division are to be traced, apparently without exception, to the *medullary substance* of the *cerebral lobe* of the same side, *i. e.*, they originate in the *cortex cerebri*, while those of the *inferior division* come evidently from the tractus opticus, *i. e.*, from the *retina*, forming the so-called *middle-root* of the tractus, to be referred to again below. The latter set of fibres pass from

the medullary substance of the tractus between the external corpus geniculatum (fig. 271, c) and the basis cruris (P), about 12 mm. in front of the posterior border of the tuberculum posterius, into the substance of the thalamus. The perfect similarity which thus exists between the modes of connection of the thalamus, on the one hand with the *retina*, and on the other with the *cortex cerebri*, seems to entitle the former to be considered as a nervous centre of equal morphological significance with the latter. The propriety of this view of the significance of the retina is confirmed by the fact that the mode of origin of the centrifugal tracts of the crus cerebri in the thalamus is totally unlike that of the fibres of the tractus opticus, which indicates a want of analogy between the tractus opticus and the peripheral nerves, and between the retina and the terminal structures of these nerves, that is not less striking than the analogy which has been shown to exist between these parts and the medulla and cortex cerebri. Further, in connection with the similarity referred to, between the mode of termination in the thalamus of the fibres from the *cortex cerebri* and from the *retina*, may be mentioned the fact, which has been recognized even by Arnold, that the tractus opticus takes part in the formation of the stratum zonale of the thalamus, which is otherwise derived exclusively from the first member of the projection-system, *i. e.*, from the cortex cerebri.

The connection which exists between the posterior regions of the thalamus and the occipital and temporal lobes has already been treated of (p. 679).

The tegmentum cruris cerebri springs in threefold manner from the thalamus opticus: 1, in the form of the fibres of the *posterior commissure;* 2, in the form of the *laminæ medullares;* 3, in the form of the fasciculus from the *ganglion of the habenula conarii.* The region of origin of the last-mentioned fasciculus only (Figs. 271, H, 264 I), is to be traced externally. It projects at the inner border of the stratum zonale, as an oblong, club-shaped body, invested by fibres which constitute its portion of the superior member of the projection-system. The thick crural fasciculus that springs from the ganglion of the habenula (H') bends, under cover of the gray substance which lines the 3d ventricle, into an S-shaped curve, so as to pass first to the outside of the poster. longit. fasciculus (L), and then to the inside of the centrum rubrum of the tegmentum, some of its fibres often traversing the latter, and then turns upon itself at a right angle just behind the substantia nigra, to continue its course as the most anterior and interior fasciculus of the tegmentum. It may be that the fasciculus of one side is derived from the stratum zonale of the opposite ganglion, the fibres having crossed the median line in the posterior commissure. The ganglion habenulæ is larger in animals than in Man. Its nerve-cells are heaped closely together, giving it a different structure from that of the rest of the thalamus, and resembling that of the pineal gland itself.

The two other regions of origin of the tegmental fibres in the thalamus are not separated the one from the other, but are nevertheless to be distinguished by the peculiarities of their structure, as two districts which might be separated by a line passing from the outer border of the tuberculum anterius to the outer border of the ganglion of the habenula. The inner of these artificial divisions would be the *region of origin* for that part of the *crus cerebri* which is derived from the *posterior commissure*, the outer the *region of origin* for that part which is derived from the *laminæ medullares.*

It is the fibres passing from the cerebral lobes into the thalamus by way of the *anterior and inferior pedicles*, that run longitudinally through the inner district of the thalamus (fig. 270, J K) and enter the posterior

commissure, a fact which cannot be demonstrated on section preparations, by reason of the inward bend which the fibres make as they enter upon the latter half of their course, but which may be traced by following up the fibres in properly hardened preparations. These fibres are disposed in layers, which alternate regularly with layers of gray substance of about the same thickness with themselves, and in the cells of this gray substance (which are spindle-shaped, 30 μ long by 10 μ broad, and which lie parallel to the fibres) they terminate their course as cerebral fibres, and proceed again as crural fibres. To be more explicit, the fasciculi of the posterior commissure, having passed about 5 mm. beyond the median line, run directly forwards to join the tegmentum (fig. 270, *Ch*), within which they pursue their further course downwards, to take part finally in the formation of the spinal cord.

The posterior *external* district of the thalamus bears a certain resemblance, in point of structure, to the nucleus lenticularis, for here as there the medullary fibres from the *cerebral lobes*, as they pass in radiating lines toward their terminal cells, are intersected in their course by concentric fibrous laminæ which, in both ganglia, are made up of fibres destined for the *crus cerebri.* Of these concentric laminæ within the thalamus (fig. 271, T'), anatomists have given their attention to the innermost only, which Burdach designates as *lamina medullaris*, and which is described as separating the so-called external and internal nuclei of the thalamus. Since, however, the lamina medullaris is almost strictly confined to the posterior half of the thalamus, these supposed nuclei are, at least in the anterior half of the thalamus, no longer to be distinguished. Luys describes this medullary lamina as enclosing, in the midst of the substance of the thalamus, a nucleus called by him the centrum medianum, which is thereby sharply defined, posteriorly, superiorly, inferiorly, and externally (fig. 271, *Cm*). The cells of this mass do not differ in form or size from those of the rest of the thalamus. It receives its entering fibres from the anterior pedicle of the thalamus. This lamina medullaris, however, which encloses the inner nucleus of Burdach, the centrum medianum of Luys, is no independent formation, but only the innermost of a number of medullary laminæ, which contain bundles of fibres that run directly into the tegmentum cruris cerebri of the same side, without crossing the median line, as do those which pass through the posterior commissure. These crural fibres, which on cross-sections may be demonstrated to surround, in their further course, the cerebellar portion of the tegmentum, its *centrum rubrum* (rothen Kern) (fig. 271, $R\ K$ with T), bear the same relation to the radiating fibres of the thalamus which are derived from the retina (fig. 271, $II\ R$), and to the radiating fibres derived from the cortex cerebri (fig. 271, R).

While the anterior regions of the thalamus rest immediately upon the fasciculi of the internal capsule, or, in other words, upon the basis cruris cerebri, which is still in process of formation (fig. 268), farther backwards two fan-shaped fibrous expansions from the corona radiata make their way between the basis cruris and the thalamus into the substance of the latter. The fibres composing the upper of these fan-shaped groups form, by their convergence, a cylindrical body that becomes the centre of organization for its respective half of the tegmentum, and which receives the name of *red centre* of the *tegmentum*, because it takes up among its fibres a large number of nerve-cells (which are for the most part very small), and thereby swells to a ganglionic mass (figs. 269, 270, 271, 272, $R\ K$). This red centre constitutes the first nodal mass in the course of a nervous tract which begins under the form of the above-mentioned group of fibres from

the corona radiata, and ends in the cortex cerebelli. The *processus cerebelli ad cerebrum* (Bindearme) constitute an exposed fragment of this connecting tract between the two cortices.

The second and more slender fan-like expansion of fibres, situated below the first, attaches itself to the pointed, outwardly-directed extremity of the substantia nigra of Soemmering, whose relation to the basis cruris has already been discussed. After the entrance of these groups of fibres, the thalamus lies directly upon the crus cerebri (Fig. 271), one of whose two parts, the basis, presents a fully formed structure, while the other, the tegmentum, becomes a complete structure only on the arrival of certain fibres destined for the spinal cord, which are contributed by the corp. quadrig. and its neighboring ganglia. The *corp. quadrigem.* and *thalamus opticus*, besides being in connection with the crus cerebri, both receive fibres, in common with the corpora geniculata, from the tractus opticus. The general description of the corpus quadrigeminum may be preceded to advantage by an examination of its anatomical relations in these two last mentioned respects, as thereby the discussion of the thalamus, as well as of the other cerebral ganglia, is closed, while the corp. quadrigem. forms a border-station, and belongs in part to the next section of the encephalon, viz. : the pons Varolii, which we are to examine later. In the regions where the *tractus opticus begins*, or, more properly speaking, where it *terminates its course*, the posterior extremities of the thalami (tuberculi posteriores, die Polster) diverge from each other, thereby leaving room for the insertion of the corp. quadrig., and project beyond the limits of the crura cerebri, which lies more toward the median line. Instead of upon these latter, the posterior tubercle rests upon the two corpora geniculata (fig. 272, *Th*, *Gi*, *Ge*), and the fasciculi of the stratum zonale of the thalamus converge towards the commencement of the tractus opticus. In fact the stratum zonale is, as we have seen, made up of these fasciculi which come through the tractus from the retina, and of an arched tract of fibres which come from the medullary substance of the temporal lobe, and run parallel with the tractus. The tractus has then a twofold connection with the thalamus, once by way of the *superficial* fibres just mentioned, and again by way of the *deeper-seated* fibres described on p. 694.

The corpus geniculatum externum shows, on cross-section, a broad, heart-shaped, *i. e.*, bilobate surface, which characteristic is, in fig. 272, *Ge*, not sufficiently pronounced. *J. Wagner* must have looked upon one of these fibres as constituting a special formation, for he describes a certain well-defined nucleus of the optic nerve in the thalamus, which he represents as if made up of alternate layers of gray and white substance, which is nowhere to be found except in the corpus geniculatum externum. The gray substance of the corpus geniculatum externum occurs in laminæ, and not in rounded masses, as does that of the other ganglia, and these laminæ are folded together in zigzag fashion, as if in order to pack them into a closed capsule of medullary substance. If the structure of the optic nerve in the Fish be taken as a guide, where the gray matter is in like manner disposed in folded laminæ, the signification of the structure of the external corpus geniculatum may be interpreted as follows :—A layer of gray substance may be imagined as lying between two layers of medullary substance, one of which represents the medullary substance of the tractus, and the other the medullary substance of the hemispheres. The fibres of the medullary laminæ may then be supposed to have entered into connection with the cells of the interposed gray substance, and the two opposed sets of laminæ to have been then folded together in zig-zag fashion. Thus it is brought to

pass that laminæ of gray and white substance would alternate continually with each other, as is seen to be the case in the corpus geniculatum externum, in whatever direction the section be made. The cells of this ganglion are 30—48 μ in length and 15 μ in breadth, and are for the most part coarsely granular, and contain pigment. That portion of the tractus

Fig. 272.

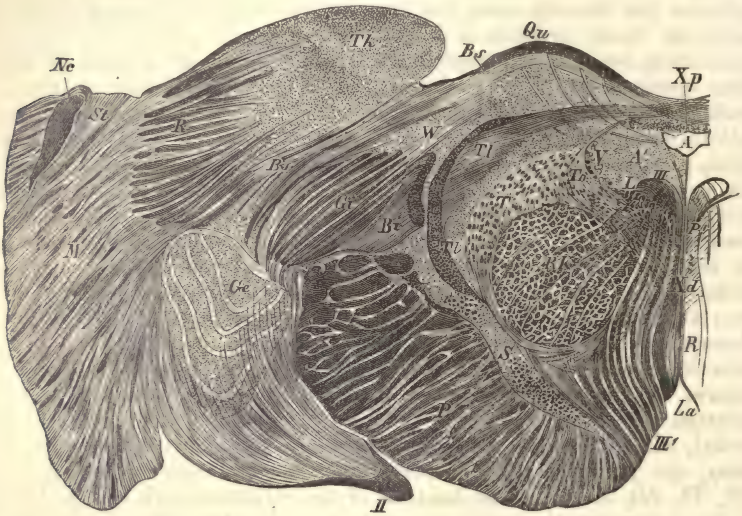

Fig. 272.* *Transparent cross-section from the ganglia of origin of the tractus opticus* in the Human brain. *M*, the medullary substance of the cerebral lobes ; *II*, tractus opticus ; *R K*, centrum rubrum tegmenti (rother Kern der Haube) ; *Nc*, nucleus caudatus ; *St*, stria cornea ; *Th*, tuberculum posterius thalami optici ; *Qu*, corpus bigeminum superius (oberer Zweihügel) ; *Gi*, corpus geniculatum internum ; *Ge*, corpus geniculatum externum ; *S*, substantia nigra ; *A*, aqueductus Sylvii ; *A'*, central tubular gray matter surrounding the aqueductus ; *R*, median raphe of the tegmentum ; *La*, lamina perforata posterior ; *R'*, bundles of fibres entering the tuberculum posterius ; *Bs*, brachium corporis bigemini superioris ; *Bi*, brachium corporis bigeminum inferioris. The most inferior bundles of the corpus geniculatum internum which come from *Bi*, are seen to enter the tractus opticus. *W*, root of the optic tract, from the corpus bigem. superius, transmitted by the corp. genic. internum ; *Xp*, roof of aqueductus Sylvii, occupied by the decussation of the brachia corp. bigem. superioris, after which the right brachium passes on to join the stratum lemnisci of the tegmentum (Schleifenschicht der Haube) (*H.*) ; *Xd*, decussation which takes place anteriorly to the aqueductus, between the fibres which originate in the quintus cells *V*, and make their way through the tegmentum ; *III*, roots of the oculo-motorius ; *T*, district of the tegmentum containing the fibres destined for the spinal cord ; *V*, cross-sections of the fasciculi of the descending root of the 5th cerebral nerve, with the bladder-shaped cells that lie at the side of them ; *L*, posterior longitudinal fasciculus ; *III*, common nucleus of the nervus oculo-motorius and the nervus trochlearis ; *P'*, fibres from the crus cerebri, that traverse the raphe (*R*) and terminate in the nucleus just mentioned.

which stands in connection with the external corpus geniculatum, lying to the inside of the superficial set of fibres which connect it with the thalamus opticus, and to the outside of the deep set, is of considerable size (fig. 272, *II*).

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* *R*, on the left of the figure should be *R'*.—Transl. Note.

The relation of the two corpora geniculata to the occipital and temporal lobes has already been treated of (fig. 266, page 678.)

Inwardly from, and for the most part, also, anteriorly to the external portion of the tractus that has just been described, lies the portion which is connected with the oval or spindle-shaped corpus geniculatum internum, which ganglion conducts the fibres of the tractus, by which it is traversed as if by meridian lines, to both the *superior* and the *inferior corpus bigeminum.* The spindle-shaped cells, 25 μ in length and 5 μ in thickness, of which the ganglion is composed, effect at the same time a reduction in the number of these fibres. The fibres that thus connect the tractus opticus with the superior corp. bigeminum, pass in diverging rays inferiorly and somewhat posteriorly to the brachium corp. bigem. superioris, into the small nerve-cells of the ganglion (fig. 272, *Gi*, *W*).

Besides this mediate connection between the corpus quadrigeminum and the tractus opticus, a direct connection is effected by fibres that may be traced from the tractus directly into the brachium *corp. bigem. inferioris.* No more convincing argument could be found for the propriety of regarding the optic nerve as morphologically a part of the cortex cerebri, and not a peripheric nerve, than is furnished by the fact that a portion of its fibres thus attach themselves to the *arm of the inferior corpus bigeminum*, which is essentially nothing but a fasciculus of the corona radiata, having its *origin* in the *cortex cerebri*, and its *termination* in the said *ganglion* (fig. 272, *Gi*, *Bi*).

Connected as it is with both divisions of the *corp. quadrigem.*, the *internal corpus geniculatum* keeps the same relative position to these ganglia, in point of development, throughout the Mammal series. The size of the internal corpus geniculatum maintains also a constant proportion to that of the tegmentum itself, probably not alone on account of the relation of this ganglion to the corp. quadrigem., but also because it is itself really one of the ganglia of origin of the tegmentum, by reason of the fibres which it sends to join the arm of the inferior corp. bigem.

The innermost fibres of the tractus opticus in part embrace the basis cruris, in part intertwine themselves with the outermost fasciculi of the latter. (Fig. 271.) The further course of this group of fibres is not known to me. I can, however, say with certainty that they do not, as appears at the first glance, and as Burdach believed, unite with the substantia nigra, though the latter certainly lies very near them. On the contrary, they always seem to terminate suddenly, near, or posteriorly to, this ganglion.

The *region of the corpus quadrigeminum* lies inwardly from the so-called optic region (Sehursprung), and consists of three superposed and fused divisions, disposed about the aqueductus Sylvii, which lies somewhat superiorly or rather posteriorly to a plane dividing the whole region under consideration into two equal parts (fig. 272 *A*). Above (or behind) the aqueduct lies the corp. quadrigem. proper, having between its two halves the roof of the aqueduct. In front of the aqueduct (if we imagine ourselves looking at a cross-section) lie first in order the tegmenta cruris cerebri, fused together at the middle in the raphe (*R*), and having for their inferior surface the lamina perforata posterior (*La*). Laterally from and anteriorly to the tegmenta, lie on either hand the lowest divisions of the region marked out by the corpus quadrigeminum, the basis cruris cerebri. The corp. quadrigeminum is made up of a superior and an inferior pair of ganglia, which, taken together with their respective brachia (the fasciculi sent to them from the cortex cerebri by way of the corona radiata), have, in general terms, a transverse position in the encephalon. The brachia inferiora preserve by no means strictly this transverse position, for, acting

as the axis for the arch-shaped thalamus opticus, they are pushed forward by the posterior tubercle of the latter (fig. 266 *Bi*). The masses of ganglionic substance of the corp. quadrig. are enclosed between a superficial (fig. 272 *Bs—Xp*) and a deep-seated (fig. 272 *Xp—Tl*, 264, *m'*) layer of medullary substance. The superficial layer forms a sort of *stratum zonale*, such as invests the thalamus opticus, made up of fibres of the brachia corp. quadrigem., which is the only set of fibres belonging to the first member of the projection-system that are visible upon the surface of the brain. The deep-seated layer of medullary substance contains the fibres contributed by the corp. quadrigem. to the tegmentum. The superficial medullary system of one side is continuous with the deep-seated system of the other, and they are all consequently fused together at the middle line. Within the posterior fifth of the length of the corp. quadrigem., the deep-seated medullary substance is no longer to be distinguished as a separate layer. having lost its compactness by being spread through the gray substance of the ganglion (fig. 273 *Q*). A processus corporis quadrigemini ad cerebellum certainly exists, probably made up of fibres from the brachia after their decussation, although this designation is by no means deserved by the tract to which it is usually given (the processus cerebelli ad cerebrum, Bindearm). It properly belongs to the frenulum veli medullaris, which consists demonstrably of two similar halves, and which runs, by way of the valve of Vieussens, into the superior vermiform process of the cerebellum.

A cross-section of the medullary substance of the corpus quadrigeminum which passes through the middle line of the ganglion (*i. e.*, a median longitudinal section of the ganglion in its natural position), shows the former to be directly continuous with the medullary substance of the posterior commissure (fig. 264 *m'*). This posterior commissure is, however, in connection not only with the thalamus, as has been described, but also with the ganglionic substance of the *pineal gland* (conarium), and with that of its pedicle, the habenula. This entire medullary formation of the posterior commissure appears on a longitudinal section of the brain (fig. 264, *m'*, *Z*, *Z'*) as an S-shaped appendix to the central part of the medullary substance of the corpus quadrigeminum. The lower curve of the S is formed, 1. by the cross-section of the groove made by the posterior commissure, its opening looking backwards, its upper curve (2) continuous with the lower by the section of the medullary substance of the *conarium*, which, as the fibres curve round, parallel with its surface, also appears as a groove whose opening looks forwards, and the beak of the S by the *ganglion habenulæ* of one side or the other, together with its longitudinal fibres that divide off the thalamus opticus from the gray substance lining the 3d ventricle, and that, according to *Arnold*, *Luys*, *Jung*, *Inzani*, *and Lemoigne*, stand in connection with the fornix also. In the early stages of development in the Human brain, and permanently in many Mammal brains, the pineal gland itself, as well as its pedicle, is split into two halves (Luys).

Burdach and Arnold have found true commissural fibres in the posterior commissure.

The pineal gland has often, but improperly, been compared to the hypophysis cerebri. Luys regards it as a prolongation of the gray substance of the third ventricle. Arnold very properly declared it to be separated by its medullary substance from that gray substance. It should in truth be considered as a ganglion, and, like the ganglion of its pedicle, which is similarly constructed, it is connected on the one hand with the medullary substance of the cerebral lobes, and on the other, by means of the posterior commissure, with the crus cerebri. It may then be reckoned among the *ganglia*

of origin of the *tegmentum*. It contains cells of two different sizes, the one 15 μ in thickness, the others very small, only 6 μ in thickness, and its structure only differs from that of the other cerebral ganglia in that its cells are crowded very closely together. In the habenula, layers of cells often alternate with layers of nerve-fibres, a formation which calls to mind the alternating layers of granules and fibres in the bulbus olfactorius. The neighborhood of the medullary substance, as well as the universal presence of processes, characterize the cells described as nervous elements. The crowded arrangement of these cells is like that of the cells in the stratum corporum arctorum of the cornu ammonis, and this peculiar mode of arrangement and minute size is found also among the cells of the olfactory lobe, the cortex cerebelli, and certain cell-masses in the corpus striatum. The latter ganglion contains also collections of larger nerve-cells.

The fibres of the first member of the projection-system from the cortex cerebri enter the corpus quadrigeminum by way of the brachia corp. bigem. superioris (fig. 272 *Bs*) et inferioris (fig. 272 *Bi*, 273 *B* ×). The brachium corp. bigem. superioris traverses the thalamus opticus just above the two corp. geniculata, leaving between itself and them a portion of the substance of the thalamus which, on sections, appears triangular (fig. 272, *Bs*, *Ge*, *Gi*).

The fibres of the brachia corp. quadrigem. terminate, perhaps, like the fibres of the corona radiata in general, in the ganglion of the same side with the hemisphere from which they spring. The median decussation between the fibres of the two sides takes place after interruption of the fibres by the cells of the corp. quadrigem., or, in other words, takes place between spinal cord fibres, which have sprung from the substance of the ganglion.

That which has just been said respecting the mode of termination of the brachia corp. quadrigem. undoubtedly holds good as regards those fibres that plunge at once into the midst of the substance of the ganglion, and it may also without hesitation be assumed to be true of the fibres that take part in the formation of the stratum zonale of the corpus quadrigeminum, for the reason that the cells of the corp. quadrig. are not confined exclusively to the gray substance of the special nuclei, but are scattered abundantly through the external layers of the stratum zonale, so that the component fibres of the latter are by no means obliged to penetrate into the substance of the gray nuclei, which would be possible only after they had crossed the median line in order to find their terminal cells. It is not so easy to discover the course adopted by the most anterior fibres of the brachium corp. bigem. as respects their decussation, inasmuch as on cross-sections from the brain of the Ape, these fibres are seen to pass through the thalamus opticus, not as a compact group, but separated irregularly from one another by the substance of the latter, whereas they are collected into a compact fasciculus as they traverse the superior corpus bigeminum. It is, however, probable (although the matter needs further investigation), that the fibres in question do end in the ganglion of the corp. quadrigem. of the same side, and they perhaps accomplish it by bending, when in the neighborhood of the median line, and running backwards, *i.e.*, downwards parallel to the same, to decussate at a later period. The probability of the truth of this explanation is strengthened by the fact that, in longitudinal sections through the corpus bigeminum superius, certain fine longitudinal fibres are to be seen, distributed through the gray substance (fig. 264 *Q'*) and running from the point of the entrance of the brachium corp. bigem. superioris towards a more posterior portion of the median line, where they decussate.

It has already been remarked that the brachium corp. bigem. inferioris

is joined, during its passage through the corp. geniculatum internum, by fibres from the tractus opticus.

The gray substance lining the inner surface of the corpus quadrigeminum belongs, like that on the inner surface of the thalamus opticus, to the *central tubular gray matter.* This gray substance surrounds the aqueductus Sylvii, as a continuation of that which lines the 3d ventricle. Here, too, the description of the ganglia of the corp. quadrigem. should be preceded by a description of this gray substance, because, since the two masses lie so near each other, and are so intimately connected, the signification of the former will thereby be made, in certain respects, more intelligible. The central tubular gray substance surrounding the aqueductus Sylvii is limited posteriorly by the decussating medullary fibres of the corp. quadrigem., anteriorly by the posterior longitudinal fasciculus (hinterer Längsbündel) (figs. 272, 273, A', Xp, $B\times$, L). It is bordered laterally, within the limits of the corp. bigem. superius, by well-defined fibres, which are on their way to join the tegmentum, while in the region of the corp. bigem. inferius it is not less sharply bordered by a system of fasciculi which run more or less parallel with the aqueductus, and which show on cross-section a chain of cut surfaces (fig. 273, $5'$) that lies externally to the posterior longitudinal fasciculus. These fibres, which constitute the descending root of the quintus, become gradually developed from the cells surrounding the aqueduct. The lumen of the aqueduct, which differs at different levels, has been, together with its lining of cylindrical epithelium, described by Gerlach. If the ring of gray substance that surrounds it, as seen on cross-sections, be divided into two half-rings by a transverse line, drawn in the region of the corp. bigem. superius just in front of the aqueduct, in the region of the corp. bigem. inferius through the aqueduct, the posterior half-ring will be found to be peopled with small cells 25 μ in length and 5 μ in breadth, and the anterior half-ring by large cells 30—50 μ in length, 15—25 μ in breadth. The larger nerve-cells occur partly dispersed, partly quite compactly disposed. Under the latter form they constitute, in the region of the upper corp. bigem., the common nucleus of origin of the oculomotorius and trochlearis, which is bordered by limiting fibres, and which, in the region mentioned, lies posteriorly to, and in the region corresponding to the upper half of the corp. bigem. inferius, in an excavation in the posterior longitudinal fasciculus. To the same region belong also, in fact, the systems of scattered cells in the neighborhood, which, lower down, are not to be distinguished from the collections of cells which people the eminentia teres.

The *common nucleus of the oculo-motorius and trochlearis* stands in connection: 1. With the *fibræ rectæ* of the raphe (fig. 272, *III P*), of whose component fibres, in so far as they do not terminate in the cells which lie scattered in the raphe itself, the innermost radiate in diverging lines among the dispersed cells belonging to the above-mentioned nucleus, the central and external ones pass into its compact portion, the nucleus proper. In so doing, these fibres describe curves whose convexities are directed outwards, and the innermost somewhat smaller cells of the nucleus are disposed with their long axes strikingly parallel to these curves. The fibræ rectæ of one side decussate at acute angles with those of the other side. They have their origin in the nucleus lenticularis, and form (as already described) the most inferior stratum of the ansa peduncularis, then the innermost fasciculus of the basis cruris. They bear the same relation to the nucleus of the oculomotorius and trochlearis, that the fibres which cross with the anterior pyramids bear to the nuclei from which spring the anterior roots of the spinal

nerves. They are the shortest of the constituent fibres of the crural system, because, originating as they do in the nucleus lenticularis, they terminate peripherally in that part of the central tubular gray matter that contains the nuclei from which spring the most superior pair of the motor cerebral nerves.

2. From the substance of this common nucleus of the oculo-motorius and trochlearis, in which these fibres terminate, spring the roots of the oculo-motorius nerve (fig. 272, *III'*), being fibrous bundles of considerable thickness, which run forward through the substance of the tegmentum to the inner side of the crus cerebri, curving outwardly (as if in continuation of the curves described by the fibræ rectæ), and passing partly through, partly to the inner side of the red centre of the tegmentum. The entire course of the fibres which terminate in the oculo-motorius furnishes us with a simple scheme which may be applied to the course of the great mass of fibres of which the projection-system is in part made up, those which run by way of the anterior division of the crus cerebri, its basis, to the collective motor-nerve roots of the whole cerebro-spinal system. The superior member of this simple typical projection-tract consists of the respective fibres of the corona radiata that terminate in the nucleus lenticularis; its second member, of the fibres which, springing from that ganglion, run for a certain distance in the basis cerebri, cross the middle line as fibræ rectæ of the raphe, and terminate in the nucleus of origin of the oculo-motorius nerve, which latter forms the third member of the same projection-tract. The size of the fibrous bundles, the number of their component fibres, and the calibre of the individual fibres, are all much smaller in the bundles that enter from the crus cerebri into the nucleus of the oculo-motorius, than in the nerve-roots that pass off from the same nucleus, a fact which is in accordance with the statement made by Deiters, which certainly in many cases admits of confirmation, that a change in the structure of the nerve-fibres accompanies the interruption of their course by the cells of every central ganglionic nucleus.

3. From the same nucleus spring the roots of the nervus trochlearis. The decussation of this pair of nerves (*i. e.*, of the fibres that make up the nerve-tract of which the trochlearis is the peripheral portion) takes place, as Stilling has demonstrated, not previous to their entrance into the nucleus, but after the formation of the nerve-roots proper, and immediately before their exit from the brain, in the valve of Vieussens just below the corpus quadrigeminum (fig. 274, 4).

According to this view of the case, it would seem probable that the fibres which connect the trochlearis with the cerebral lobes do not decussate, as do those which run to the oculo-motorius under the form of fibræ rectæ of the raphe, unless we assume, as physiological observations do not justify us in doing, that a second, reversed decussation takes place. The roots of the trochlearis spring principally from the compact portion of the common nucleus, and especially from that part of it which lies below the rest, in an excavation in the posterior longitudinal fasciculus, and their fibres converge in the form of a pencil. On cross-sections made through the upper half of the lower corpus bigeminum, these fibres are seen surrounding and forming a border for their nucleus posteriorly. In the region of the lower half of the same ganglion, these converging bundles come together and form a compact fasciculus, whose transversely cut surface is to be seen on cross-sections through the ganglion at the extremity of the transverse axis of the ring of gray substance surrounding the aqueduct of Sylvius (fig. 273, 4).

The entire course of the trochlearis, whose nucleus of origin lies anterior to the aqueduct and in the region of the upper corp. bigem., while its final

point of exit lies behind the aqueduct and below the lower corp. bigem., must of necessity lie in a plane which inclines downwards and forwards from the point of origin of the nerve, and encircles the aqueduct of Sylvius (Stilling). Misapprehending their real character, Stilling and Deiters have

Fig. 273.

Fig. 273. *Transparent cross-section passing through the lower half of the corpus bigeminum inferius and the upper portion of the pons Varolii.* Human brain. *A*, the aqueductus Sylvii enclosed within its central tubular gray substance; *Q*, the ganglion of the corp. bigem. inferius; *Bs*, decussation of the brachia corp. bigem. inferioris; *S*, pedunculus corp. bigem. infer. (lemniscus); *m*, superior lamina of the lemniscus, from the corp. bigem. superius; *Ba*, processus cerebelli ad cerebrum, in process of decussation; *Vs*, fibres destined for the spinal cord, lying to the inner side of the processus cerebelli ad cerebrum; 4, cross-section of one of the trochlearis roots; *L*, posterior longitudinal fasciculus; 5, cells of the substantia ferruginea; 5′, descending roots of the 5th pair, with the bladder-shaped cells from which they spring; *P*, continuation, in the anterior section of the pons, of the basis cruris cerebri; *Trp*, deep-seated transverse fibres of the processus cerebelli ad pontem; *Trs*, superficial transverse fibres of same.

described certain descending roots of the 5th nerve, which certainly lie very near the trochlearis at the point of exit of the latter, as a so-called inferior division of the roots of the latter nerve (fig. 274, 5).

Even within the limits of the upper corp. bigem., the central tubular gray matter encloses nuclei that give rise to the *motor nerve* roots referred to, which lie more or less near the *median line;* also a *laterally disposed* sensory nerve tract, the roots of the 5th cerebral nerve. The fibres composing these roots originate at the outermost border of the gray matter that surrounds the aqueduct of Sylvius, in small collections of large bladder-shaped cells 60 μ in length and 45—50 μ in breadth (fig. 272 *V*), and form themselves by degrees into a series of bundles whose transversely-cut surfaces, succeeding each other like the links of a chain (as seen in cross-sections made in this

region), lie in a curved line around the outer edge of the thick wall of gray substance which surrounds the aqueduct (figs. 273 and 274, 5′).

Fig. 274.

Fig. 274. *Transparent cross-section from the Human pons Varolii, showing the nervus trochlearis at its exit.* *A*, central tubular gray matter enclosing the aqueductus Sylvii; 4, decussation of the nervus trochlearis in the velum medullare anterius. 4′, cross-section of a trochlearis root; 5, substantia ferruginea; 5′, chain of the cross-sections of the descending roots of the 5th pair; *L*, posterior longitudinal fasciculus; *BA*, cross-section of the processus cerebelli ad cerebrum, becoming compact again, after their decussation; *VS*, fibres destined for the spinal cord, lying to the inner side of the processus cerebelli ad cerebrum; *m*, stratum lemnisci from the corp. bigem. superius; *S*, stratum lemnisci from the corp. bigem. inferius.

The cell-masses from which spring the two kinds of nerves, motor and sensory, have then, even in the region of which we have been treating, the same general position in relation to each other that they retain throughout the whole extent of the central tubular gray matter, those connected with the motor nerves lying in the neighborhood of the median line, and towards the anterior part of the ring of gray substance, while those connected with the sensory nerves are placed laterally and at the same time towards the posterior part of the same ring, and the nerves of this region thus become anatomically analogous to the anterior and posterior spinal nerves.

In the pons Varolii and oblongata there appears, as Deiters has pointed out, another system of nerves, an *intermediate, lateral system*, whose roots lie between those of the median (anterior) nerves and those of the lateral (posterior) nerves.

The cells from which spring the above-mentioned roots of the 5th pair differ strikingly, in respect to their shape, from the cells in the common nucleus of the oculo-motorius and trochlearis. The former cells are inflated, bladder-like, and furnished with but very few and slender processes, which project abruptly from the cells like the straw from a soap-bubble. The latter are large like the former, but slender, and rich in processes whose calibre passes by gradual transition into that of the cells. The former resemble the cells of the spinal ganglia, the latter those of the anterior cornua of the spinal cord. Indeed, it is not the difference in size, but a morphological characteristic of another kind, that serves thus to distinguish, among these cells, the sensory from the motor.

Running from the upper border of the epithelium that lines the aqueduct of Sylvius to the median groove of the corp. quadrigem., there is to be seen, especially in the lower Mammals, a dark line, a sort of seam, which I have been able to recognize in the Cat as consisting of a layer of fibrous connective tissue furnished with vessels, that divides into two layers which pass outwards at the upper edge of the aqueduct, just as the layer of connective tissue in the posterior fissure of the spinal cord divides into two layers. The thread-like extremities of the posterior epithelial cells of the aqueduct extend themselves toward it. In Dogs, I have found star-shaped and

oblong cells in this lamella. A trace of the same lamella is to be seen in the Human brain, especially in the region of the lower corp. bigem.

As regards the *ganglionic masses* of the *corp. quadrigem.*, those of the *superior corp. bigem.* have each, on cross-section, the shape of a plano-convex lens, whose lower surface rests upon the fibres which are on their way outwards and forwards from the point of their decussation to enter the crus cerebri, while those of the *inferior corp. bigem.*, more delicately but more clearly defined, are shaped like double convex lenses, and are bounded inferiorly by the innermost of those fibres which they themselves send to join the crus.

The *size* of the *nerve-cells* of the corpus quadrigeminum is subject to great variation. In general the smaller among them, 15–21 μ in length and 5 μ in breadth, are the ruling forms, and the superficial layers of both corp. bigem. are peopled exclusively by this variety. In the deeper layers, however, and especially towards the median line, there are to be found (perhaps in preponderance in the region of the super. corp. bigem.) very large cells, 45–90 μ in length and 10–30 μ in breadth. The principal axis of the nerve-cells may lie in one of three directions: 1, parallel with the surface of the ganglion, as is most pronounced within the limits of the superficial distribution of the brachia, for example, along the convexity of the inferior corp. bigem.; 2, in an antero-posterior direction, as is seen in that part of the superior corp. bigem. which lies near the median plane. The position of these nerve-cells is in keeping with the course of those fibres of the brachium corp. bigem. superioris that run so far backwards before reaching the place of decussation, as described (bottom of p. 701, fig. 264 Q'); 3, in the direction of lines radiating outwards from the aqueduct as a centre.

One set of cells, whose axes have the last-mentioned general direction, seem to be, in virtue of their position and relations, especially important to the formation of a correct idea of the structure of the corp. quadrigem. When the deep-seated layer of medullary substance, that separates the ganglionic gray matter from the central tubular gray matter, is examined on cross-section (fig. 264, m) under high magnifying powers, it is seen to be traversed by a number of fine, straight fibrillæ. In the course of these fibrillæ are inserted long, spindle-shaped cells, 45 μ by 10 μ, and the two establish a nervous connection between the gray matter of the corp. quadrigem. and the gray matter around the aqueduct, in which latter the nuclei which give rise to the motor nerves of the eye are embedded. Thus connected, the two sets of ganglia form a single nervous centre, as it were, and this anatomical union is in keeping with the physiological fact that an influence is exercised by the retina, when brought into a condition of excitement, upon the muscular system of the globe of the eye. Just as the fibræ rectæ furnished to the nucleus of the oculo-motorius belonged to the basis cruris of which they were the shortest fibres, so may these straight fibres be regarded as belonging to the fibrous system of the tegmentum cruris, inasmuch as they play for that nucleus the part which other fibres of the same system play for the nuclei of origin of the spinal nerves, viz., that of bringing them into connection with the ganglia of origin of the tegmentum itself.

The crus cerebri springs in similar manner from the superior and from the inferior corp. bigeminum. From the same ganglionic masses that received the brachia corp. quadrigem. emerge bundles of fibres that, in decussating at the median line with those of the opposite side, form the dense nervous substance of the raphe, which is the continuation back-

wards of the medullary substance of the posterior commissure. The fibres that form the indirect prolongation of the *brachium corp. bigem. super.* pass, after their decussation, forwards and upwards, in delicate fasciculi, in which small, elongated cells, 18 and 25 μ by 5 μ, lie scattered obliquely and outwards. They collect themselves finally into a fibrous layer, which on cross-section presents a crescent-shaped surface. This layer of fibres, which is at first covered in by the brachium corp. bigem. inferioris, forms the *superior lamina* of the *lemniscus* (figs. 272, *Te*, 273, *m*). The fact that nerve-cells are scattered among the fibres of this formation, even after it has become a part of the tegmentum, indicates that the number of these same fibres is continually on the increase. The fibres contributed by the *corp. bigem. inferius* to the *tegmentum* run forward in fasciculi that, under the form of the *inferior* lamina of the *lemniscus*, are in part covered over by a sickle-shaped segment of the superior lamina of the lemniscus, but that form to a great extent the exposed outer surface of the tegmentum. This layer of fibres covers immediately the processus cerebelli ad cerebrum of the same side, which, at the level of the origin of the former in the corp. bigem. infer., has already completed its decussation and is on its way towards the outer surface of the tegmentum (figs. 273 and 274 *m*, *S*, *B*, *A*).

The tegmentum cruris, which is directly continuous with the posterior region of the pons, is not, strictly speaking, in a condition of complete organization even at the lowest extremity of the crus cerebri, but continues to receive additional fibres within the uppermost section of the pons. In the region of the corp. quadrigem. the stratum formed by the lemniscus is not so broad as to reach to the median raphe, but comes to an end at a distance of about 5 mm. from it (fig. 272, *m*). In the upper part of the region of the pons, however, this fibrous stratum, the most anterior of all the formations of the tegmentum, by which the rest of the tegmentum is, as it were, supported, reaches actually to the raphe (fig. 274, *m*).

This increase in size is by no means brought about by a pushing inwards of the superficial layer of the stratum lemnisci, but, as Stilling observed, by the actual accession of a group of fibres which are contributed by the basis cruris cerebri, and which fill up the gap between the stratum of the lemniscus and the raphe. This takes place in the following manner: While the compact formation of the basis is being split up into secondary fasciculi by the transverse fibres of the processus cerebelli ad pontem (fig. 273), the most posterior fibres of the latter divide off a certain portion of the hindermost longitudinal fibres of the basis cruris, leaving them to continue their course as the above-mentioned innermost portion of the stratum of the lemniscus, and in consequence as a part of the tegmentum. Although this last group of fibres is associated alternately with the basis and with the tegmentum cruris, it is recognized as, without doubt, belonging in fact to the tegmentum, the posterior tract of the caudex cerebri, inasmuch as it does not take part in the *decussation* of the *anterior pyramids*, as do all the other spinal-cord fibres belonging to the basis cruris.

There must be, then, a certain region within the ganglia of origin of the basis cruris which is as yet undiscovered, and which should be classed among the ganglia of origin of the tegmentum cruris. The ganglia of origin of the tegmentum have been described as characterized by the meeting within them of the extremities of sensory and motor nerve-tracts, a peculiarity which distinguishes these ganglia from those connected with the basis cruris, and thereby assists materially to the formation of a correct idea of the duplex character of the origin of the spinal cord. We have seen, however,

that, within the domains of the ganglia of origin of the basis cruris, there is a region which, by means of the fibres from the olfactory lobe, is in connection with one of the sensory surfaces of the body, and *vice versâ*, just as the retina is in connection with the gray matter of the thalamus opticus. This region is the inferior portion of the caput corp. striati, just above the lamina perforata anterior. It is characterized by its structure, which differs, in respect to the form and disposition of the nerve-cells, from that of the corpus striatum proper, as not belonging morphologically to the ganglion in which it is embedded. The possibility that this region may give rise, in part, to fibres destined for the basis cruris cerebri, may perhaps suggest the direction in which a thorough investigation might advantageously be made, concerning the origin of those fibres of the stratum lemnisci (so called by Reichert) which are not derived from the corp. quadrigem.

The organization of the *tegmentum* is then finally complete, at the level which corresponds to the lower boundary of the most inferior of its ganglia of origin. It consists as described, 1. of the processus cerebelli ad cerebrum, which in the region of the superior corp. bigem. is inflated (by the addition of nerve-cells) to the centrum rubrum of the tegmentum, and in the region of the inferior corp. bigem. becomes freed of these cells; 2. of the posterior longitudinal fasciculus which springs from the ganglion of the ansa peduncularis; 3. of fibres derived from the thalamus opticus of the opposite side which have crossed the median line in the posterior commissure; 4. of fibres also from the thalamus, but which, without having crossed the median line, pass into the tegmentum by way of the laminæ medullares; 5. of the fasciculus from the ganglion of the habenula, which perhaps does not cross the median line; 6. of fibres which have crossed from the pineal gland of the opposite side; 7. of the superior lamina of the lemniscus, from the superior corp. bigem.; 9. of the above-mentioned posterior fasciculus from the basis cruris cerebri.

Above the level of the region where the fibres of the processus cerebelli ad cerebrum intertwine themselves among those of the tegmentum, as will presently be described, the latter is traversed, within the region of the superior corp. bigem., by a tract that terminates peripherally in the *larger root* of the *fifth cerebral nerve.* The larger root of the fifth nerve holds, to that region of the tegmentum in which this process now to be considered takes place, and to certain of the fasciculi destined for the antero-lateral columns of the spinal cord, the same relation that the posterior roots of the spinal nerves hold (as will be further described) to the medulla oblongata, in that region in which the future antero-lateral columns of the spinal cord are traversed by the fibres which run from the posterior columns. The large cells, that give rise to the descending root of the fifth pair, described at p. 704, which lie in clusters embedded at the external border of the central tubular gray matter around the aqueduct of Sylvius, give rise also to a striking system of fibres that encircle the latter. They may be designated, collectively, as the communicating quintus-tract (Quintusstränge). This tract is made up of fasciculi which, disposed one above the other, form a continuous delicate (about 150 μ thick) medullary wall, which surrounds the aqueduct throughout almost the entire region of the corp. bigem. superioris. Somewhat below the transverse diameter of the aqueduct, these fibres cease to lie one above the other, and range themselves side by side, occupying, on cross-sections, a considerable space, to attain which new position the bundles of fibres diverge in the form of a water-jet, and make their way, partly through the tissues lying between the posterior longitudinal fasciculus and the red centre of the tegmentum, partly to the outside of this red centre

among the mass of fibres running from the thalamus opticus to the spinal cord; in other words, through all parts of the tegmentum at that level, except the stratum derived from the lemniscus. The first-mentioned set of these fibres may then be seen to cross the median line, and, curving around the lower periphery of the red centre, to pass some little distance outwards, under the form of the so-called *fibræ arcuatæ.* Before as well as after their decussation, these *fibræ arcuatæ,* thus derived from the communicating tract of the fifth nerve, enter into connection with nerve-cells 60 μ in length by 15 μ in breadth, and in the adult Human brain containing pigment, by means of whose processes the tracts that are to become the motory columns of the spinal cord are brought into connection with these same arch-shaped fasciculi of the quintus-tracts.

In looking back over the organization of the tegmentum and its ganglia, we can discover in the structure of the latter two peculiarities, that mark them as differing fundamentally from the ganglia of the basis cruris, and that assist us in recognizing the differences in the functions of these two tracts that constitute finally the spinal cord.

In the first place, the ganglia of origin of the tegmentum are characterized by enclosing, within one and the same collection of gray matter, the termination of the tractus opticus and the origin of motor spinal tracts, and further by effecting a connection, through the agency of multipolar nerve-cells, between the communicating quintus-tracts and the motor-tracts just mentioned, as having for their function the conversion of centripetal excitation into motion. The ganglia of the basis cruris, on the other hand, not being connected with any sensory surfaces, must depend for the excitation to the performance of their functions upon another source, viz., the conditions of excitation of the cerebral lobes.

In the second place, the ganglia of the tegmentum are remarkable as being foci in which the necessary mechanism is provided anatomically for the production of special, definite motions, for which the exciting cause is again furnished in the above-mentioned centripetal excitations. The peculiarity of their structure in this respect consists in the fact that the modes of origin in the spinal cord tracts in these ganglia are so varied, and further in the fact that one and the same ganglion contributes to these spinal-cord tracts fibres, of which a part cross the median line to the opposite side, while another part remain uncrossed (thalamus opticus, for example). It might be expected as a result of this anatomical arrangement, that an impulse communicated to the ganglion of one side would call into play at the same moment the action of unsymmetrical muscles of the two sides of the body, in such a manner as might be necessary for the production of certain definite co-ordinate movements. The belief in the existence of such pieces of co-ordinating mechanism has already been expressed by Schroeder V. D. Kolk, who based his opinion upon the supposed fact that the abducens nerve is supplied by fibres from the cerebral ganglia of the same side, while those which give rise to the oculo-motor have crossed the median line, a point to which we shall recur again below.

The fibres of each basis cruris, on the other hand, spring, without exception, from the ganglia of the same side, and, in so far as they are destined for the spinal cord, they all have, as will appear below, a common place of decussation, *i. e.*, in the course of the anterior pyramids of the medulla oblongata.

The ganglia of the basis cruris cerebri seem, therefore, not to be foci for the production of co-ordinated movements, such, for example, as would require the simultaneous action of unsymmetrical muscles of the two halves

of the body. If such movements are to be produced by way of these ganglia, they must first be planned, as it seems, within that nervous centre from which the ganglia receive their (centrifugal) impulses, within the cerebral lobes, which are provided for the purpose with their fibræ arcuatæ, or association-systems.

4. The Region Occupied by the Passage of the Processus Cerebelli ad Pontem through the Projection-System.

The consideration of this part of the subject should properly be preceded by a study of the anatomy of the *cerebellum* itself, that centre which, in the region to be considered, becomes intimately connected with the projection-system by means of its processus ad pontem, that make their way transversely through the latter, and by means of certain collections of nerve-cells. The description of the cerebellum, however, which at best can be but very imperfect, will be made easier of comprehension if it be preceded by a statement of the relations in which this organ stands to other parts of the encephalon, whereby we may get an insight into its functional significance, in one respect at least.

Regarded externally and from below, the region occupied by the interlacement of the fibres of the projection-system with those of the processus cerebelli ad pontem embraces the pons and the upper half of the oblongata. If the lower surface of the brain in Man and in most of the Apes be compared with those of the other Mammal brains, important differences will be observed in almost every case, not only in the relative development of the different parts, but even to all appearance in their morphological significance. The brain of the aquatic Mammals only exhibits in this region a conformation similar to that of the brain of the Apes and of Man.

The differences in the size of the parts are caused by the small degree of development, in the lower Mammals, of the pons Varolii and the anterior pyramids on the one hand, and on the other by the excessive fulness of development in the same animals of the posterior division of the oblongata, the prolongation of the tegmentum cruris cerebri. The differences in form are these. In the Human brain, upon the surface of the region in question of the oblongata lie three longitudinal prominences: 1, the *anterior pyramids*; 2, the *olivary bodies*; 3, the *inferior peduncle of the cerebellum*; while in the brain of the lower Mammals there appears in the first place, at the sides of the pyramids, a body which is apparently wanting to the Human brain, the *corpus trapezoides*, a thick, prominent, transverse band, which extends round the oblongata as far as to the pedunculus cerebelli. On the other hand, the olivary body of the Human oblongata seems to be wanting in that of the lower animals.

A sort of hybrid formation characterizes the brain of the Ape (Pavian) in this respect, inasmuch as the corpus trapezoides and olivary bodies exist there side by side, although both are but slightly developed. In the Lemur, however (Lemures), I found the corpus trapezoides alone.

It is, nevertheless, easy to convince one's self that these parts are in reality neither wanting nor exceptionally present, but that quantitative variations in their development give rise to this deceptive appearance. The corpus trapezoides consists, in fact, of transverse bundles of fibres that lie behind the pyramids, and that, in the Human brain, are concealed by the pons (which in Man is very long), while in the brain of other Mammals they lie exposed. So also the olivary body is really to be found on cross-section

of the oblongata of all Mammals, but in most cases it lies hidden behind the anterior pyramids, instead of appearing externally by their side.

Further, a little thought will make it clear that these *variations in the form of the parts in the region of the oblongata are but the natural consequence of the differences in the degree of development between the cerebral lobes of Man and those of the other Mammals*, so that we cannot but recognize the presence of a far-reaching morphological harmony, in point of size, between the highest and the lowest divisions of the encephalon.

The key to this morphological harmony is contained in the fact, discussed in the preceding pages, that the basis cruris cerebri keeps perfect step, as regards its development, with the cerebral lobes.

For if the size of the basis cruris be dependent on that of the cerebral lobes, and if, as has been mentioned, a certain proportion of the fibres of the basis cruris pass, by way of the anterior section of the pons, into the cerebellum, which accounts for the diminished size of the prolongation of the basis at its emergence from the pons under the form of the anterior pyramids, then it is plain that the length of the pons must be in direct proportion to the size of the basis cruris cerebri, and, consequently, to that of the cerebral lobes. In the Human brain, therefore, the pons is long; in that of other Mammals it is short. Since, however, the development of certain of the deeper layers of transverse fibres in the pons is independent of the development of the basis cruris cerebri, they will, under certain conditions,—*i. e.*, when the latter tract, and, in consequence, the anterior transverse fibres of the pons, are but slightly developed,—appear uncovered, behind and at the sides of the anterior pyramids. This happens in some degree in the Ape, whose cerebral lobes are but imperfectly developed; more fully in the Lemures (Lemur) and *in the lower Mammals* these deep-seated transverse fibres of the pons appear as the *corpus trapezoides*. In Man, on the other hand, where the continuation of the basis cerebri, the anterior pyramids, require, because of their comparatively great size, quite a large space within the limits of the oblongata, they crowd to the surface the olivary bodies, which in the lower animals lie behind the pyramids and in the neighborhood of the median line, and *these displaced olivary bodies lie exposed by the side of the pyramids.*

It should be further mentioned in this connection that the development of the lateral regions of the cerebellum is in direct proportion to that of the cerebral lobes, and that the development of a certain ganglion of the cerebellum, the *nucleus dentatus*, which keeps pace with the latter in its growth, is in direct proportion to that of the olivary bodies. The absolute size of these latter, then, must increase with the increase in the size of the hemispheres, and their prominence on the surface of the oblongata must be thereby made greater.

The Processus Cerebelli ad Cerebrum, with the Velum Medullare Anterius.

The expression, "passage of the processus cerebelli through the projection-system," does not strictly define the process which characterizes the region which is its seat, for in truth the great part of the fibres that branch off from among those of the projection-system, and into the processus cerebelli in general, did not first become associated with the latter tract within the limits of the pons and upper half of the oblongata, as might be supposed, but formed a part even of the crus cerebri. This is most strikingly true of the processus cerebelli ad cerebrum, which was associated with even still

higher sections of the projection-system, having formed a part of the cerebral medullary substance, the corona radiata, before its fibres were gathered into the centrum rubrum of the tegmentum.

The process to be considered consists then essentially in the disengagement of the fibres of this processus cerebelli ad cerebrum from the projection-system, that they may pass into the cerebellum as an independent tract, and in the course of this process the arrangement of the constituent bundles of this fibrous tract passes successively through the following phases.

Although, as has been said, the bundles of fibres composing the processus cerebelli ad cerebrum were forced apart, in the region of the crus cerebri above the corp. quadrigem., by the introduction of a mass of finely granular gray substance, containing nerve-cells of two general sizes (some 45 μ by 15 μ, others 15 μ by 3 μ), and were thereby made to form the centrum rubrum tegmenti, the same processus appears in the region of the lower half of the superior corp. bigem. as a simple medullary tract, the circumference of which, by reason of the loss of the granular gray substance, must manifestly be less than that of the centrum rubrum.

This medullary tract has, however, freed itself from the connective substance of the centrum rubrum only; it continues to contain large numbers of nerve-cells, and the latter still remain scattered among its fibres even after its decussation. These nerve-cells, which are of great size (45 μ by 15 μ), are disposed in a striking and unusual manner, inasmuch as they lie parallel rather to the smallest arteries and the capillaries than to the nerve-fibres. They appear to be in the closest apposition with the walls of these vessels, are suitably bent to fit the angles made by their branches, and send out long and thick processes that run longitudinally along, and probably in, their walls. This peculiar arrangement is to be demonstrated even in the centrum rubrum itself, and from there onwards to beyond the point of decussation of the processus, and the latter does not entirely free itself of nerve-cells until it has emerged from the corp. quadrigem. These cerebral capillaries seem thus to constitute, in the midst of the central organ itself, a periphery for the termination of the cell-processes, and further investigation will show whether this crural portion of the processus cerebel. ad cerebrum is the only scene of such an arrangement.

Examined by means of successive cross-sections, the processus cerebelli ad cerebrum may be seen to approach very near to the median raphe. The surfaces which it presents on such sections, however, are never made up exclusively of the cut ends of longitudinal fibres, but, even in the region above the lower half of the superior corp. bigem., contain also a large number of transverse lines, which correspond to such fibres of the processus as have left their longitudinal course to pass over to the opposite side of the tegmentum, decussating at the median line with those that cross in the reverse direction. The region occupied on the transversely-cut surface of the tegmentum by these decussating fibres, lies between the posterior longitudinal fasciculus and the stratum lemnisci, the remaining spinal fasciculi of the tegmentum having been all pushed away by them from the neighborhood. After their decussation, the fasciculi of the processus run outwards until they reach the inner surface of the inferior lamina of the lemniscus (that which comes from the inferior corp. bigem.), which latter forms for them a sort of cover.

The nearer this decussation and the subsequent process of reconstruction of the processus cerebelli ad cerebrum (which takes place in the region of the lower half of the inferior corp. bigem. and of the place of exit of the

nervus trochlearis) comes to its completion (figs. 273 and 274, *A*), the more strictly the decussating fibres become confined to the anterior half of the posterior division of the pons. The processus of the two sides, taken together with the decussating fibres, come thus to have the form of a horseshoe opening backwards, which encloses between its two branches the comparatively large area occupied by those constituent fibres of the tegmentum destined for the spinal cord, which lie between the posterior longitudinal fasciculus and the stratum lemnisci. Only a small portion of these fibres remain unenclosed, viz., those which lie in front of the decussating processus, between them and the stratum lemnisci on either side. The position of all the spinal-cord fibres of this region is governed completely by that of the processus, which, in the course of their decussation, force their way among the former and push them aside in such a manner that, so long as the processus occupy a central position in the tegmentum, the remaining fibres lie to the outside of them, whereas when the processus attain a lateral position, the other fibres appear, on cross-section, between them.

At fig. 275, a new phase in the course of the processus under consideration is to be seen. After having completed its decussation, which is undoubtedly, as Stilling declared, complete, and not simply partial, as Arnold later affirmed, each processus disengages itself, superiorly and externally, from the posterior division of the projection-system in which it was embedded (fig. 275). Before it reaches the point corresponding to the greatest convexity of the pons Varolii, the processus still remains covered by a part of the inferior lamina of the lemniscus (*S*), which anteriorly is of considerable thickness (fig. 275, *S A*, on the left hand side); opposite the greatest convexity of the pons it lies entirely free. Opposite the region occupied by the central course of the 5th pair it has already buried itself in the medullary substance of the cerebellum (fig. 276, *A*), where it is at first covered over by the other processus of the cerebellum, but enters later into connection with the gray substance of the nucleus dentatus.

During the exposed part of their course, the processus cerebelli ad cerebrum form the lateral boundary walls of the 4th ventricle, but after their fusion with the cerebellum they form a part only of the thick medullary roof with which the cerebellum provides that cavity. At that part of their course that lies between the corp. quadrigem. and the cerebellum, the processus cerebel. enclose between them the *valve of Vieussens* (velum medullare anterius) (figs. 273, 275, *V*), with which they form, to use Burdach's expression, the *connective system* (Bindesystem) of the cerebellum. This valve of Vieussens, the prolongation of the frenulum veli medullaris, is the part that, as Arnold has shown, really deserves the designation of processus cerebelli ad corpus quadrigeminum, which has been wrongly applied to the processus cerebelli ad cerebrum.

In the velum medullare, three different systems of medullary fibres lie woven together. 1. The great mass of its substance is composed of the fasciculi of the frenulum. 2. At its anterior extremity the decussating fasciculi of the nervus trochlearis, which are of great thickness, intertwine themselves transversely among those of the frenulum (fig. 274, 4). 3. The velum medullare further contains longitudinal fibres from the superior vermiform process of the cerebellum; they decussate before quitting the limits of the latter, and after traversing the valve of Vieussens almost to the lower border of the corp. quadrigem. they turn on themselves, describing curves with their convexity looking upwards, join the inferior lamina of the lemniscus as its hindermost fasciculus, and pass onward with the latter, in the posterior division of the pons Varolii, to the spinal cord.

This latter system of fibres in the valve of Vieussens either appears so often as an anomalous formation that Hirschfeld commits no great blunder in figuring it as a normal occurrence, in his plates on the anatomy of the brain, or else it is really constant, and only less conspicuous externally in some brains than in others.

Since, as will be shown below, the cerebellum sends no fibres directly to the antero-lateral columns of the spinal cord, but on the other hand gives rise to a great part of its *posterior columns*, it is to be inferred that this innermost or hindermost fasciculus of the inferior lamina of the lemniscus, which traverses the valve of Vieussens as described, is destined also to join the *posterior* spinal columns.

Even were the appearance of these questionable fibres in the valve of Vieussens to be regarded as a very common anomaly, still, if they be considered as really a part of the extensive system of fibres that the cerebellum sends to take part in the formation of the posterior columns, from the main body of which they have wandered away to follow for a certain distance an abnormal course, the anomaly would be one that would not violate, in any essential particular, the normal structural type, whereas it would involve an actual violation of the normal type were a set of fibres to pass *occasionally* from the cerebellum to the antero-lateral columns. The processus cerebelli ad cerebrum itself remains by no means free from the admixture of foreign elements during the whole of its course to the cerebellum. At the level of the region of origin of the fifth pair, the processus is in part traversed, and in part covered, by the bundles of fibres passing from the cerebellum to the greater root of that nerve (figs. 275 and 276 *A′* 5 *d*), and further down, as will be described later, it is traversed by bundles of fibres belonging to the nervus acusticus, which form indeed a group of some size.

The Processus Cerebelli ad Pontem, with the continuation of the Basis Cruris Cerebri.

Like the processus cerebelli ad cerebrum, so the processus cerebelli ad pontem also are represented even in that portion of the projection-system that lies within the cerebral lobes.

Inasmuch as the number of the fibres that radiate from the cortex cerebri into the nucleus lenticularis and nucleus caudatus is greater than that of the fibres that spring from these ganglia in the form of the basis cruris cerebri, the collective fasciculi of the latter must be regarded as a mediate prolongation of the respective portion of the corona radiata, including those fasciculi that, instead of passing by way of the anterior pyramids to the spinal cord, branch off from the projection-system in the region of the pons Varolii, and enter the cerebellum.

At the same time that the basis cruris cerebri becomes split up into secondary fasciculi, by the passage through it of the transverse fibrous tracts of the processus (figs. 273, 275, 277, *Trs*, *Tr O*, *P*), the size of the individual fasciculi also becomes reduced by reason of the fact that after the latter have still further divided into bundles of very small size, a certain number of their component fibres come to an end by entering into connection with nerve-cells (30 μ in length and 12 μ in thickness), which cells are in connection likewise with the fibres of the processus ad pontem.

These nerve-cells are to be found not only along the borders of the districts occupied by the secondary groups of longitudinal fibres belonging to the crus cerebri, where the latter lie in contact and evidently in connection with

the transverse fibres of the processus cerebelli ad pontem, which are interwoven amongst them, but they are also to be found: 1. toward the more central portions of the secondary groups of longitudinal crural fibres, which indicates that these groups are everywhere penetrated by the fibres belonging to the processus ad pontem, and 2. within the strata that contain the exclusively transverse fibres of the processus, viz., both the superficial and the deep transverse fibrous layers of the anterior division of the pons. In this latter position they cannot be supposed to serve any purpose except that of interrupting the course and increasing the number of the cerebellar fibres in one direction or another.

We may divide the transverse fasciculi belonging to the processus ad pontem, as they appear on the surface of the pons obtained by cross section, into —1. a superficial stratum; 2. those interwoven among the longitudinal crural fibres; 3. a deep-seated stratum (figs. 275 and 277, *Ts*, *P*, *Tp*). One is tempted to assume that only the second of these three divisions is concerned in conducting to the cerebellum the longitudinal crural fibres *with which its own are interwoven;* the other two divisions, and especially the deep-seated stratum, seem to be entirely out of connection with the projection-system and to act only as a commissure for the hemispheres of the cerebellum, and at the same time, if such were their function, their peculiar arrangement would still remain a mystery. Certain considerations oblige us, however, to abandon the conception of these superficial and deep transverse fasciculi as tracts that, ranged one behind another, simply cross from one processus ad pontem to the other, and to regard them as following a more complicated course, even those of the deep-seated layer being, in fact, in common with all the constituent fibres of the entire transverse system, connected by means of the cells above referred to with the fibres of the projection-system. The following are three of these considerations:—1. The deep-seated stratum of transverse fibres has its upper boundary at a lower level and its lower boundary at a higher level than does the superficial stratum, for which reason the latter projects somewhat beyond the former, both at the superior and at the inferior edge of the pons, leaving small cavities behind it, the foramina cæca. This may be fairly accounted for on the supposition that the deep-seated transverse fibres spring from the nerve-cells of this region of the pons, in which, as described, the fibres belonging to the crus cerebri terminate. In virtue of this arrangement, at the superior edge of the pons, where none of the crural fibres have as yet entered into connection with these cells (fig. 273), and at its inferior edge, where this process has ceased and where the formation of the anterior pyramids is already completed, the transverse fibres of the deep layer, which have their origin at the termination of the crural fibres, would be wanting; whereas, toward the middle of the region of the pons, where the crural fibres terminate in the greatest numbers, this deep stratum would be (as in fact it is) in its fullest state of development. 2. Fasciculi that belong to the central division of the transverse system, made up of those which are interwoven with the longitudinal fasciculi, may be seen to cross over and join the deep transverse stratum of the opposite side, after running backwards for a certain distance in the median line. In all the cross-sections that include the deep transverse layer, bundles of fibres are to be detected curving around the outer side of the general mass of longitudinal crural fasciculi (from the central to the deep transverse stratum). (Figs. 275, right-hand side, and 277.) Having passed the middle line once, *i. e.*, having come from the processus ad pontem of the opposite side and made their way, as a part of the central division of the transverse fibres, between the longitudinal fasciculi, these bundles of fibres

pass the median line for the second time in the opposite direction, as fasciculi of the deep stratum, to return into the very processus of which they originally made a part. This fact suggests as plausible the following general theory of the course of the component fibres of the processus:—Each fasciculus, after leaving its respective processus, crosses the median line as a part of the superficial transverse stratum of the pons, makes its way among the anterior longitudinal fasciculi of the opposite side, and enters into connection with the latter by means of nerve-cells. It then curves around the outer side of the groups of longitudinal fasciculi, enters the deep stratum of the transverse fibres, crosses the median line for the second time, and runs through the same processus to which it first belonged, back again into the cerebellum. Following, in the light of this hypothesis, the course of the crural fasciculi through the region of the pons, we may say in general terms that *each fasciculus of the basis cruris cerebri that terminates in either side of the anterior division of the pons, is represented in the cerebellar hemisphere of the opposite side by two fasciculi, one of which runs* with the superficial, the other with the deep stratum of the transverse system of fibres from the point of their connection with the crural fasciculus into the processus cerebelli ad pontem of the opposite side. If this be true, then each basis cruris cerebri, besides being brought into connection with the opposite half of the spinal cord by means of the decussation of the anterior pyramids, is also brought into connection with the opposite hemisphere of the cerebellum through the agency of these fibres, which cross into the opposite processus cerebelli ad pontem. Since each basis cruris cerebri sympathizes, as a rule, in the atrophy of the cerebral lobe of the same side, it may be that the connection just described between the basis cruris and the opposite cerebellar hemisphere accounts for the complication of such an atrophy of one hemisphere of the cerebrum with atrophy of the opposite hemisphere of the cerebellum.

Pedunculi Cerebelli Inferiores, with the Continuation of the Tegmentum.

The pedunculi cerebelli contain the third stratum of fibres which interweave themselves transversely among the longitudinal fasciculi of the projection-system. The relation which the pedunculus cerebelli bears to the projection-system differs from that borne by the two last-mentioned fibrous systems by which the latter is traversed, in that while the *processus cerebelli ad cerebrum* constitute a connecting tract, that seems only to traverse the projection-system, and while the *processus cerebelli ad pontem* serve to conduct a portion of the second member of the projection-system *into the cerebellum*, the *pedunculi cerebelli inferiores* bring an addition of considerable size to the *projection system*, or, to speak more exactly, convey a contribution of fibres from the *cerebellum* to the *posterior columns of the spinal cord*. Each pedunculus cerebelli is divided, according to Stilling, into an *outer* and an inner division. In his great work on the pons Varolii, that has fairly broken the path for the study of the anatomy of the brain, he makes the outer division (fig. 280 *M F C*), the *corpus restiforme*, a fasciculus of considerable size which emerges from the cerebellum at a point which, measured on the pons Varolii, corresponds to the region between the origins of the superior and inferior roots of the facial nerve (fig. 277, *Cr*, fig. 278, *St*). The corpus trapezoides of the lower Mammals, and the stratum zonale which invests the surface of the oblongata, and especially the olivary bodies, are formed of fibres derived from the superficial layers (figs. 280, 281, *ZZ*) of this fasciculus.

The inner division of the pedunculus cerebelli emerges from the cerebellum at about the same level with the corpus restiforme (figs. 277, *Z C*, and 278, *H*) and forms a tract of fine bundles of fibres which, on cross-section, appears as a four-sided surface, lying to the inner side of the oval surface presented by the former tract (fig. 280 *S F C*). Stilling committed an error in regarding this inner division of the pedunculus cerebelli as the commencement of the fasciculus gracilis and the fasciculus cuneatus of the spinal cord. The dimensions of the former tract, which descends immediately from the cerebellum (figs. 277, 278), are much less considerable than those of the fasciculi gracilis et cuneatus, and the structure of the two tracts is very different, the inner division of the pedunculus consisting of small fasciculi embedded in a diffused collection of gray substance, which contains very large nerve-cells (figs. 280 *S F C*, 281 *Gr*, and *Cn*). By the side of the fasciculi grac. et cuneat., which on cross-section appear as if distended by the masses of gray matter which they enclose, and whose fibres are arranged, in the inner portion of the tract made up of the two fasciculi, after the manner of wicker-work, in its outer portion more compactly, the pedunculus remains always distinguishable, although constantly diminishing in size as it passes downwards. If then, on the one hand, Deiters is not justified in denying that any portion of the fibres, which make up the inner division of the pedunculus cerebelli, are derived directly from the cerebellum, still, on the other hand, it is quite probable that these fibres do not reach, under the form of the inner division of the pedunculus, the respective posterior column of the spinal cord, but that, even above the point of closure of the central canal, they resolve themselves into fibræ arcuatæ of the oblongata. At any rate, before the disappearance of this inner division of the pedunculus, it becomes wedged apart from the corpus restiforme by the introduction between them of that fibrous formation which, together with the masses of gray substance which it encloses, and which so distend it that it forms on the surface the prominences of the fasciculi gracilis et cuneatus, really passes over into the posterior column of the same side of the spinal cord. It will be explained below that these medullary fasciculi are, on each side, the *indirect prolongation* of the *corpus restiforme of the opposite side*, the latter diminishing progressively in bulk at the same rate at which they increase.

The pedunculus that seems externally to be continuous with the respective posterior column of the cord, is made up, therefore, of the following distinct formations: 1. The corpus restiforme. 2. The inner division of the pedunculus cerebelli. 3. The fasciculi gracilis et cuneatus.

These formations are to be seen side by side, in that part of the oblongata that lies between the limits which correspond to the sections represented in figs. 280 and 281.

The Posterior Tract of the Projection-System.

The explanation of the manner in which the *pedunculi cerebelli* weave their fibres among those of the *projection-system*, with the two sides of which they lie in apposition, must be preceded by a description of the mosaic-like arrangement, at various levels, of the constituent formations of the latter as seen on cross-sections.

In the region where this posterior tract of the projection-system (the tegmentum) has freed itself, which takes place in the upper third of the region of the pons, from the processus cerebelli ad cerebrum, by which it had been traversed, *i. e.*, after the latter have made their way to the outer sur-

face of the posterior division of the pons, where they form the lateral boundary walls of the 4th ventricle (fossa rhomboidea) (fig. 275 *A*), cross-sections of the same tract, which may here be called the posterior division of the pons, show the following new formations to have associated themselves with those which have been described in connection with the crus cerebri, as comprising the different sets of fibres contributed by the ganglia of origin of the tegmentum to the antero-lateral columns of the spinal cord. These additional sets of fibres are: 1. the prolongation of that portion of the lemniscus which is derived from the corp. bigem. inferius, the "*pes lemnisci*" (figs. 275 and 276, *S*); 2, the **ascending root of the 5th pair of* nerves, the tri-facial (figs. 276 *Q*, 277, 280, 281, *S*); 3, the *pedunculus cerebelli*, just described.

Fig. 275.

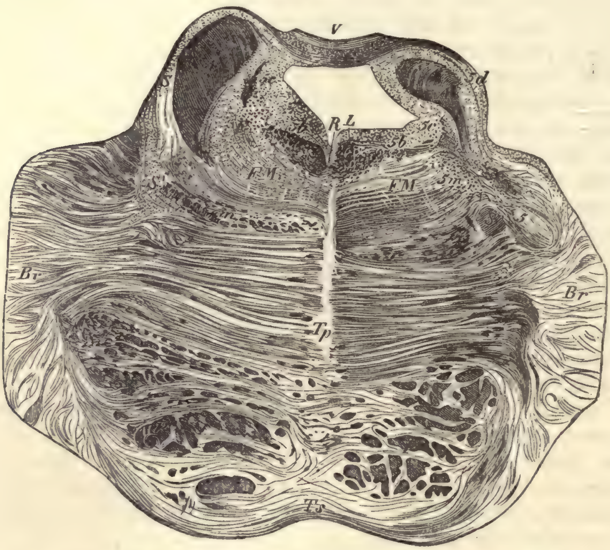

Fig. 275. *Transparent section from the Human pons Varolii, at the level of its greatest convexity. The left half of the section comes from a higher level than the right, and falls within the region occupied by the motor (smaller) root of the 5th pair.*

V, velum medullare with the lingula, roofing over the 4th ventricle, that becomes wider below (*i. e.*, as represented in the right-hand half of the figure); *A*, cross-section of the processus cerebelli ad cerebrum, as they lie in the lateral walls of the 4th ventricle; *L*, the posterior longitudinal fasciculus, lying beneath the floor of the 4th ventricle; *S*, the inferior lamina of the lemniscus, on the left-hand side of the section still covering the processus ad cerebrum, on the right-hand side appearing as a circular group of nerve-fibres, which surrounds a collection of gray substance (*S*); *FM*, the motor district of the posterior division of the pons; *S'*, the stratum lemnisci of *Reichert*; *Br*, the processus cerebelli ad pontem—*Tp*, being the deep-seated, *Ts*, the superficial stratum of its transverse fibres; *P*, cross-sections of the groups of longitudinal fasciculi of the basis cruris cerebri; *5m*, the nucleus of origin of the motor root of the 5th pair, which towards the outer part of the section are seen penetrating the processus ad pontem (5); *F*, substantia ferruginea anterior; *5b*, *5b*, bundles of fibres which come from the substantia ferruginea, make their way among

* The terms "ascending" and "descending" applied to the roots of the nerves indicate that the latter run upwards or downwards to reach the point of exit of the nerves themselves.

and around the outside of the fibres of the posterior longitudinal fasciculus, *L*, cross the raphe, and gather themselves (at the level corresponding to the right half of the section) to form the inner portion of the descending root of the 5th pair, lying to the right of the posterior longitudinal fasciculus. These fibres are joined by fibræ rectæ from the raphe that curve round the inner border of the posterior longitudinal fasciculus; 5*c*, the outer portion of the descending roots of the 5th pair; 5*d*, portions of the larger root of the 5th pair, curving themselves around the processus ad cerebrum; *R*, the raphe.

Thus constituted, the surface obtained by cross-section of the collective groups of fibres conveyed by the tegmentum to the antero-lateral spinal columns may be divided, for purposes of description, into different districts, as follows: Proceeding forwards from the gray floor of the fourth ventricle, three such districts, lying *one behind the other*, may be distinguished. The first contains the *posterior longitudinal fasciculus;* the second, *the* (middle) *motor region;* the third, the *stratum lemnisci* (*Reichert*). Again, in proceeding from the median line outwards, there may be distinguished two such districts lying *side by side*, the first being occupied by the groups of fibres destined to form the anterior spinal column, a region which borders on the median raphe and is bounded outwardly, in the pons by the roots of the nervus abducens, in the oblongata by those of the nervus hypoglossus; the second by the group of fibres destined for the *lateral column.* The latter district borders on the former, and extends outwards as far as the ascending root of the fifth pair, enclosing therefore the *pes lemnisci* (Stilling).

The posterior longitudinal fasciculus, which extends uninterruptedly through the medulla oblongata into the posterior fasciculi of the anterior spinal column (as is seen on transparent longitudinal sections through the caudex cerebri), owe the compact characteristic appearance which they present on section preparations to the great size of their component medullated fibres, which distinguishes them even in the highest regions of the caudex cerebri. The *stratum lemnisci* is characterized by similar optical peculiarities. The remaining districts of the *tegmentum* do not have this striking, compact appearance until later. According to Deiters, a change of this kind in the calibre of the nerve-fibres necessarily implies a previous interruption of their course by nerve-cells.

The remaining groups of fibres of the tegmentum attain this increased size in the following order: In the region of origin of the facial nerve, those portions of that collection of fibres described as destined to form the anterior spinal columns, which lie in the immediate neighborhood of the posterior longitudinal fasciculus, become more compactly disposed, and in the sections taken from the upper part of the oblongata this entire region, occupied by the future anterior spinal column, appears uniformly dense, while the region occupied by the future lateral column of the spinal cord presents in its central portions a similar appearance, which, as stated above, is due to an increase in the medullary substance of the nerve-fibres, but not until a later period.

The *pes lemnisci* is made up of the fibres belonging to the inferior lamina of that system gathered into a group, which, until it nearly reaches the region of the facial nerve, has a circular form (figs. 275, 276 *S*), and that encloses a compact mass of cells of the same size with those which lie between the fibres of the lemniscus, while the latter still covers the processus ad cerebrum. It is incorrect to give, as Stilling does, the designation of gelatinous substance to this mass of cells, as is proved by their size (30 μ by 12 μ), which considerably exceeds that of the elements of the latter.

From the level of the origin of the facial nerve outwards, the pes lemnisci is no longer to be distinguished by its enclosing this compact mass of nerve-cells, but contains them only scattered here and there. This tract by no means loses itself, however, in the ascending root of the fifth pair (figs. 276, right-hand side, *Q*, 277, 280, 281 *S*), as I formerly believed, but, on the contrary, cross-sections from oblongatas, where the inferior lamina of the lemniscus can be satisfactorily followed, prove that the pes lemnisci extends, under the form of the outermost fasciculus of the lateral columns, even into the spinal cord (Stilling), lying, in the pons and oblongata, at first by the side of the roots of the facial nerve (fig. 277), then in the closest apposition to the ascending root of the fifth pair. Since this root encloses gelatinous substance which is in direct continuation with the caput cornu posterioris of the spinal cord (substantia cinerea gelatinosa), in whose cells it terminates, it is plain that the continuation of the pes lemnisci must lie within the spinal cord, in apposition with this same caput cornu posterioris. Owing to the favoring circumstance that these roots of the fifth pair are, by the fineness of their constituent fibres, which contain but little medullary substance, and therefore look comparatively dark on cross-section preparations, to be clearly distinguished from the white columns of the spinal cord, it is easy to demonstrate that, at the lower end of the oblongata, this caput cornu posterioris ceases to be accompanied by them, as it had been before, and comes into immediate contact with the lateral and posterior columns, a relation which remains unchanged throughout the entire length of the spinal cord.

Genetically considered, the group of fibres that border on the anterior part of the posterior cornu (the posterior portion of the lateral spinal column) arises from the same central generative mass from which the posterior columns are derived, and should be reckoned physiologically with the centripetal tracts. May it not be that this group of fibres, which belongs thus functionally to the posterior columns, though associated anatomically with the lateral columns, is perhaps only a continuation of those fibres of the pes lemnisci that came by way of the valve of Vieussens from the cerebellum? (p. 713). If this be so, then that portion of the stratum lemnisci that arises in the corp. quadrigem. passes entire into the centrifugal tracts of the spinal cord.

To the inner side of the pes lemnisci (the continuation of the inferior lamina of the lemniscus), and behind the stratum lemnisci (continuation of the superior lamina of the lemniscus), which curves slightly to make room for it, lies the *superior olivary body** of *Schroeder v. d. Kolk* (figs. 276, 277, 278, 279, *O*), described by *Stilling* in treating of the Human brain as a ganglionic mass, supplementary to his inferior trigeminus-nucleus; by Deiters, however, recognized and designated rightly, even as it occurs in the Human subject. In Man it extends from the most superior of the roots of the facial nerve down to the lower border of the pons; in certain animals, to the lower border of the corpus trapezoides. In the brain of the Cercocebus cinomolgus I found it to be 2.5 mm. in length. In Man its outlines are indistinct; but in the Dog, for example, it appears as a well-defined body, consisting of an outer portion, which is bent into the shape of a U, and an inner portion, the *superior accessory olive*, which on cross-section has an elongated oval form. I have satisfied myself, by means of an exquisite longitudinal section from an Ape's brain, made by Dr. Clason, prosector

* The olivary body of the medulla should, strictly speaking, be designated, as it is here, as the *inferior* olivary body.—(TRANS.)

in Upsala, that the superior olive is traversed by fibres of the tegmentum, *i. e.*, of its prolongation in the posterior division of the pons, and that these fibres enter into connection with slender nerve-cells of the ganglion (30 μ by 6–9 μ), their position in the mosaic work of cross-section preparations being *behind the stratum lemnisci and to the inner side of the pes lemnisci.*

The *inferior olivary body*, which belongs to the upper half of the medulla, attains in the Human brain, through the enlargement and corrugation of its nucleus dentatus, its highest degree of development. Indeed, Schroeder v. d. Kolk believed the superior and the inferior olivary bodies of the lower Mammals to be united in the inferior olive of Man, which is however a mistake. The so-called accessory olivary bodies (external and internal) have precisely the same structure with the nucleus dentatus, being made up of finely granular gray connective substance with multipolar nerve-cells, 24 μ in length by 9–12 in thickness; and indeed are probably not really separated from the main nucleus, but are, on the contrary, the extremities of the latter, folded back to form the opening of the so-called hilus, which faces backwards and inwards.

The appearance of separation between the two masses may be due to the fact that the main nucleus is traversed, at the place of the apparent interval, by an especially abundant supply of transverse nerve-fibres. Reichert concluded, from the gross appearance of the cut-surface of the oblongata, that the accessory olivary bodies were nothing but blood coagula in small vessels, cut across, and discolored by chromic acid, an opinion which is certainly untenable. The inferior olive lies, with respect to the longitudinal fasciculi of the tegmentum, anteriorly to the superior olive, being embedded *in the midst of the medullary substance of the stratum lemnisci* (*funiculus olivæ* of Burdach), whose fibres, running slightly inwards and backwards, in longitudinal spiral curves, penetrate the nucleus dentatus and enter into connection with its nerve-cells, thus constituting the longitudinal portion of the medullary substance which occupies the cavity of the olivary body. Clason's beautiful longitudinal sections from the Ape's brain have entirely convinced me of the correctness of this view. Deiters also has described the olivary bodies as being connected with the spinal columns.

A certain portion of the fibres of the stratum lemnisci do not penetrate the olivary body, but merely pass over a part of its surface, and, inasmuch as they are brought into prominence by the bulging form of the latter, they have received from Burdach the designation of funiculi siliquæ (Hülsenstränge). Their relation to the nucleus is merely one of position, and they are inconstant in their occurrence, and variable as to the degree of their development.

Besides these defined masses of gray substance, the olivary bodies, and besides the collections of nerve-cells that evidently stand in connection with the roots of the cerebral nerves and later become their nuclei, there are other nerve-cells enclosed within the *motor district* of the posterior division of the pons, which are sometimes of small, sometimes of large size, irregularly disposed, and which plainly stand in connection with the fibres of the pedunculus cerebelli, by which the region in question is traversed.

The smaller elements (24–33 μ by 9–12 μ) of these systems of scattered cells are limited, essentially, to that region of the pons that lies between the place of decussation of the processus cerebelli ad cerebrum, and the region of origin of the facial nerve (figs. 275, 276, *M F*, *m*), where they form numberless small clusters that lie between the medullary fibres of the *motor district* and are especially common in the *stratum lemnisci.*

In the lower half of the pons, these cell-clusters become confined to the

neighborhood of the ascending roots of the 5th pair of nerves, into which they are undoubtedly carried by the transverse fibres by which the latter is traversed; indeed they are to be distinguished by their size as belonging to these fibres, even in the midst of the gelatinous substance which the roots of the 5th pair enclose.

In the oblongata, and, to speak more exactly, in the region of the vagus nerve, these cell clusters make their appearance again in the lateral columns, in the first place in the form of a single quite large group, situated to the inner side of the stratum lemnisci, the *nucleus of the lateral columns* (Stilling, Clarke, Deiters), and further in small groups that lie posteriorly to the olivary body and towards the median line.

In the upper part of the pons, where the smaller cells abound, the larger elements of the scattered cell-systems of the motor district are only found in very small numbers scarcely deserving of mention. In the region of origin of the facial nerve they begin to be of frequent occurrence, but lower down their number is still greater, and in that section of the medulla oblongata which has just been under consideration they are everywhere to be found.

Even within this region however, as seen in cross-section, these large cells are not distributed equally over every part of the surface. In those districts where the nuclei of the motor nerves (facialis, abducens, hypoglossus, vagus, and accessorius) are present in the greatest profusion they occur also in the greatest numbers, and moreover they are the most thickly disposed in the neighborhood of the gray floor of the 4th ventricle and in the lateral columns —in short, in the districts occupied by these very nuclei. Deiters therefore certainly did not speak without reason when he said that, besides their connection with their nuclei of origin, the nerve roots were connected with these dispersed elements, a relation of which more will be said below.

The fibrous system of the *fibræ arcuatæ* (figs. 275 to 281 *M F E*, *M F I*, *M F*, in *F M*, *V S*, and at *ar*, *a*, *A S*, *A M*) plays an important part, as appears at first glance, in the structure of that section of the posterior tract of the caudex cerebri (the continuation of the tegmentum) that lies between the level at which the decussation of the processus cerebelli ad cerebrum is completed, and that which corresponds to the lower extremity of the olivary body. The greater part of these transverse fibres, however, are derived from the pedunculus cerebelli, and as emissaries of the latter they weave themselves among the fibres of the projection-system. The rest of them are derived from the ganglia of origin of the cerebral nerves, and will be treated of below.

The course of that part of the fibræ arcuatæ that is now to be considered cannot be satisfactorily traced for all the regions in which they occur, and the greatest difficulty is met with, as may be imagined, in the region of the greatest convexity of the pons and that occupied by the main roots of the 5th pair (figs. 275 and 276), for at that level the pedunculus cerebelli has not yet made its appearance, by tracing whose course it becomes possible later to obtain an insight into the manner of termination of these fibres. The fibræ arcuatæ of this obscure region may be divided into three systems, according to their relations and course.

The 1st or *superior* system. It is certain that the fibræ arcuatæ of the superior part of this region enter into connection with the *clusters* of the *smaller nerve-cells*, and, through their agency, with the fibres of the projection-system (future antero-lateral columns of the spinal cord). It is however probable that the posterior set of these same transverse fibres direct their course backwards when they arrive near the inner surface of the processus cerebelli ad cerebrum, and thus enter the cerebellum (fig. 275, left-

hand side), while at the same time the tendency which their inner extremities show to turn forward, makes it probable that they cross the raphe and pass into the anterior set, whose component fibres, as will appear later, are all in connection with the *corpus restiforme.*

The 2d or *middle* system of fibræ arcuatæ is connected with the nucleus dentatus of the *superior olivary body*, which acquires a worm-like appearance from the transverse striation made by the passage of these fibres (figs. 279, 276, 277, 278, *o*).

Fig. 279.

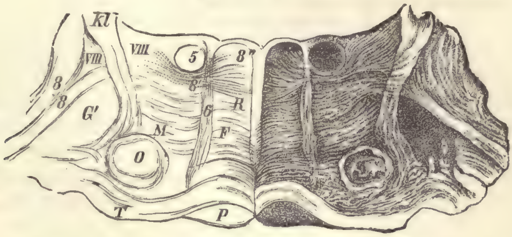

Fig. 279.* *Transparent section from the oblongata, at the level of the nervus acusticus, from Hypsiprimnus murinus.* *VIII*, nucleus of the nervus acusticus; *P*, anterior pyramid; *M F*, section of the motor district of the posterior division of the oblongata; *R*, raphe; *G′*, gelatinous substance; *O*, superior olive; *Kl*, inner division of the pedunculus cerebelli; *T*, corpus trapezoides; 5, genu nervi facialis; 6, nervus abducens; 8, roots of the nervus acusticus; 8′, fibres from the nuclei of the nervus acusticus, that lose themselves in the neighborhood of the posterior longitudinal fasciculus 8″.

The fibræ arcuatæ, which in the Human brain emerge from the restiform body immediately behind the deep stratum of transverse fibres of the pons, in the region of origin of the facial nerve, and which, passing partly in front of, partly through, the root of the 5th pair, pierce the stratum lemnisci on their way to the raphe (fig. 277 *cr*, through *S* to *R*), are morphologically identical with the corpus trapezoides (Deiters) of the lower animals, which, on account of the shortness of the pons (in the lower Mammal brains), lies freely exposed on the surface of the oblongata, by the side of each anterior pyramid (fig. 279 *T*, 278 *St*, *Rs*). After having decussated at the median line, these fibres direct their course outwards, passing behind the corpus trapezoides of the opposite side to reach the superior olivary body (fig. 278 *N* to *O*; figs. 277 and 279, *R* to *O*). By winding themselves spirally around the surface of this nucleus, they help to form for it a capsule of nerve fibres (figs. 278, 279, *O*), and then make their way transversely through its substance, entering undoubtedly into connection with its nerve-cells. Besides being united in this manner with the restiform body of the opposite side, the nucleus dentatus of the superior olivary body is further brought into connection with the cerebellum, by means of fibres that run directly into the latter, piercing on their way the inner division of the pedunculus cerebelli. These fibres pass off from the system of nerves that form its capsule, and in certain animals form so large a group as to attract the attention immediately (fig. 279 *Kl*).

* Since the plates were arranged to illustrate the description of the various anatomical systems of fibres, figs. 279 and 280 have been removed from the places that they would occupy if their natural succession had been regarded. In order however that the reader may be able to refer the sections to their real positions, they are numbered according to the order in which they anatomically occur.

They are probably to be regarded as the continuation of those fibres of the restiform body that have been described as entering the olivary body, and that, before their emergence, ran in an intricate manner around and through the substance of the latter.

I would not maintain that all the connections of the superior olivary body have been included in the foregoing description. Especially in the region of the trapezoid body, delicate bundles of fibres are to be seen ascending from the neighborhood of the latter to the outer border of the nucleus dentatus superior of the same side, which assuredly form no portion of the above-mentioned tracts, and whose origin cannot indeed be referred with certainty to the restiform body.

The third or *inferior system of fibræ arcuatæ from the pedunculus cerebelli* lies in the region of the inferior olivary body (figs. 280, 281). The relations of this last system are not so easy of demonstration as the points which we have just been discussing, concerning the connection between the fibræ arcuatæ and the superior olivary body. I see, therefore, a proof of that power of penetration of *Otto Deiters* that marks him as a true investigator, in the fact that he was able to discover between the formations of this region a relation of an entirely unexpected character, which, although subjected to the closest criticism and to repeated modification, must still be regarded as affording, in its leading features, the key to the correct comprehension of the anatomy of the district in question. Stilling, Lenhossek, and Schroeder, and, with even greater fidelity, Clarke, had described the course of the superior and inferior systems of the fibræ arcuatæ, their connection partly with the external, partly with the internal division of the pedunculus cerebelli, as well as the fact of their traversing the substance of the olivary. That, however, the restiform body and the anterior division of the fibræ arcuatæ in the region of the inferior olivary bodies, the fasciculi cuneatus and gracilis, which pass into the posterior spinal column, and the posterior division of the same fibræ arcuatæ, are but fragments of one and the same fibrous system with which the inferior olivary bodies stand in connection, no investigator before *Deiters* ventured to maintain. Lenhossek indeed emphasized his belief in the fact that the anterior division of these fibræ arcuatæ had no connection with the other parts of the system referred to, by describing them as forming a commissure between the cerebral lobes. Nevertheless, the fact that the corpus restiforme, the outer division of the pedunculus cerebelli (fig. 280 *MFC*, in fig. 281 the prolongation of *Z* behind *S*), progressively diminishes in size from above downwards, finally to disappear altogether, just at the same rate at which the funiculi gracilis et cuneatus, the posterior column of the oblongata (fig. 281 *H*, *i.e.* $Cn + Gr$), increase in size, justifies, and even forces upon us, the *conclusion* that these two tracts constitute in reality only different portions of *one coherent system*, the *posterior column* of one side having its origin *in the cerebellar hemisphere of the other side*. Taking this general conclusion of Deiters as a guide, I have unravelled the details of this connection between the different parts, as follows:—

The fibrous tracts of the oblongata, from which the posterior columns are thus formed, may be divided into two groups, each of which follows a different course.

1. The *outermost* and *middle fibræ arcuatæ* from the restiform body form a system of fibres analogous to the corpus trapezoides, in the region of the superior olivary body. Having their origin in the cerebellum, they pass in part around and to the outside of the ascending root of the 5th pair (*S*) and the olivary body, under the form of the stratum zonale, and in part they make their way through the root of the 5th pair as well as through the

olivary body, although without entering into connection with the nerve-cells of the latter. While passing transversely through the region occupied by the root of the 5th nerve, their course is interrupted by small nerve-cells, and further on they become connected with the cell-clusters of the motor district (nucleus of the lateral column of the oblongata).

Fig. 280.

Fig. 280. *Transparent section from the Human oblongata at the level of the uppermost roots of the vagus nerve.* *VIII* to X^3, transverse section of the gray floor of the 4th ventricle; *P*, anterior pyramid; *O*, inferior olivary body, with *Z*, the stratum zonale; *MFC*, the outer division of the pedunculus cerebelli (corpus restiforme); *SFC*, the inner division of the pedunculus cerebelli; *Oi*, *Oe*, nuclei olivares accessorii internus et externus; *R*, raphe; *MFJ*, inner division of the motor district (future lateral column of the spinal cord); *G*, the gelatinous substance; *S*, fibres constituting the ascending root of the 5th cranial nerve enclosed in and surrounding this gelatinous substance. *AS*, fibræ arcuatæ connected with the inner division of the pedunculus cerebelli; *Am*, fibræ arcuatæ connected with the outer division of the pedunculus cerebelli; *XII*, the roots of the nervus hypoglossus; *X*, portions of the main roots of the vagus passing through the gelatinous substance. The *X* placed beneath the gray floor of the ventricle marks certain portions of this root that emerge, in company with certain roots of the hypoglossus, from the median raphe; X^1 bundles of fibres from the posterior column of fibres from which the vagus (in part) arises; X^2, the anterior nucleus of the vagus, with fibres that run backwards toward the gray floor of the ventricle and bend round beneath it to enter the main root of the nerve; X^4, bundles of fibres that emerge from the raphe and run just beneath the epithelium of the gray floor, around and through the eminentia teres; X^3, median nucleus of the vagus; *VIII*, fibres belonging to the nervus acusticus (Clarke).

These fibræ arcuatæ then cross the median raphe of the oblongata, passing on the way in part in front of the olivary body, in part out of its hilus, and make their way into the hilus of the *olivary body* of the *opposite side, entering into connection with its nerve-cells.* This connection between the olivary of one side and the *restiform body* of the *opposite side* was assumed by Deiters on the strength of the fact that in *both olivary bodies*, besides a certain number of fibræ arcuatæ that stand in connection with the nerve-cells of the latter, as may be proved by following them up in alcoholic preparations, other fibres are to be found that simply pass without interruption through the nucleus, in curving lines. The justice of this view is confirmed by the pathological circumstance that atrophy of one *hemisphere of the cerebellum* always occurs in connection with atrophy of the *opposite inferior olivary body.* From the cells of the olivary body, the fibræ arcuatæ (rather the posterior set of them) continue their course toward the *funiculi gracilis et cuneatus*, which form the posterior column of the opposite side from that hemisphere of the cerebellum in which they originated, to become finally a component part of these longitudinal tracts, after making their way through the nuclear masses that the same enclose. The bulk of the funiculi is thereby so much increased that they approach the median line from both sides behind the central tubular gray matter of the region, so as finally to come into apposition with each other, leaving only the posterior fissure between them (fig. 281 *Gr*).

2. It is manifestly impossible that the *most posterior* of all the fibræ arcuatæ should be in connection with the olivary body of the same side with the posterior column of which they finally make a part, because, during their entire course from the raphe to the latter, they lie behind the olivary nucleus. There are however reasons for thinking that these same hindermost fibræ arcuatæ have already traversed the other olive, before reaching the raphe. It is found in fact that they do not run directly across the median line in passing from one side of the oblongata to the posterior column of the other side. On the contrary, their course is long and is directed from before backwards, or, to be more explicit, they run along the raphe in the form of fibræ rectæ during one part of their course, while during another part, *i. e.*, before they have left the anterior column to cross the median line, they run in straight lines in a direction from forwards and outwards, backwards and inwards toward the raphe, thereby traversing in all probability the region of the olivary body. It is especially this set of the fibræ arcuatæ that enter into connection with the large, irregularly grouped cells of the motor district of the oblongata. It is probable then that *the most posterior of the fibræ arcuatæ* that spring from the *corpus trapezoides* of either side, traverse the substance of the *olivary body of the same side*, but *pass behind the opposite olivary body after crossing the raphe*, and, having entered into connection with the *large, scattered cells*, they join the posterior column, their final destination.

Having reached their respective posterior columns, the collective groups of fibres whose course we have been considering lose themselves in collections of nerve-cells, within which they become organized anew into a sort of network which gives a peculiar flame-like appearance to section-preparations, and separate, below the floor of the ventricle, into two groups that are fused together anteriorly, known as the *nuclear masses* of the *funiculi gracilis et cuneatus* respectively (fig. 281 *Cn*, *Gr*). The component elements of these nuclei are for the most part of small size (24 μ by 6–9 μ), only a small but easily distinguishable semi-circular group, consisting of the outermost hindermost cells of the fasciculus cuneatus, being made up of larger elements (30–36 μ by 15 μ).

The various paths followed by the fibræ transversæ from the pedunculi cerebelli, as described above, serve moreover to place these fibres in connection with the fasciculi of the projection-system composing the continuation of the tegmentum cruris cerebri. The two systems of fibres seem by no means merely to lie side by side without further connection, but to be actually united with each other by means of the above-mentioned *clusters of small cells*, by means of the *olivary bodies*, and perhaps even by means of the *large scattered cells.*

The real significance of the relation which the systems of fibræ arcuatæ that lie above and in the region of the superior olivary body bear to the spinal tracts of the tegmentum is at present scarcely to be conjectured, perhaps because our knowledge of the morphological conditions of the case is still too imperfect. Even were it true however, as seems possible, that both these tracts terminate in the cerebellum, this fact would give us no help in deciding whether they serve to conduct in general in a centripetal or a centrifugal direction.

On the other hand, the *fibræ transversæ of the oblongata* which pass over into the posterior columns constitute manifestly a centripetal tract, and in virtue of their connection with the cell-clusters (nuclear masses of the lateral columns) that lie on the other side of the oblongata from the respective posterior columns of which they make a part, and thereby with certain of the spinal fasciculi of the tegmentum of that side, they establish a mechanism for the production of reflex action, such as exists in the ganglia of origin of the tegmentum and again in the course of the crus cerebri, where the motor fibres of the latter are connected with the 5th cerebral nerve, as described above.

It is not less probable that certain fasciculi of the projection-system that are known to pass from the crus cerebri into the olivary bodies are, through the agency of the nerve-cells of the latter, brought into connection with the spinal cord, or, by as yet undiscovered paths, into connection with the nuclei of origin of the motor cerebral nerves. *Deiters*, to be sure, regarded the longitudinal crural fibres that stand in connection with the olivary bodies as serving to prolong the posterior columns of the cord into the cerebral lobes. Such an assumption however is by no means justifiable from a morphological point of view, since, as we have seen, those fibres that pass from the tegmentum into the olivary bodies proceed from tracts (the stratum lemnisci and the motor district of the tegmentum) that are the continuation of the antero-lateral columns of the spinal cord. The belief that the centrifugal and the centripetal nerve-tracts in the projection-system remain distinct from each other would have to be abandoned altogether, if *Deiters*' view of the relation which the inferior olivary body bears to the projection-system should be accepted, which certainly should not be done without stronger reasons therefor than have as yet been afforded.

Of the possible significance of the large, scattered cells, more will be said later.

Mode of Origin of the Cerebral Nerves from the Fifth to the Twelfth.

Within the region occupied by the *passage of the collective processus cerebelli* through the projection-system of the *crus cerebri*, the latter *loses* that group of nerve-fibres which represent the muscles and the sensitive surface of the head, inasmuch as they reach their point of termination in the central tubular gray matter at this level. The cell-masses in which these fibres, the 2d member of the projection-system, thus terminate, serve also to give origin to the corresponding part of the 3d member of the projection-system, *i. e.*, to the respective cerebral nerves themselves, at the same time increasing the number of the component fibres of the nerve-tract, all of which has already been explained in speaking of the common nucleus of the oculo-motorius and the trochlearis.

That system of nerve fibres that represents the cerebral nerves in the crus cerebri, like that which is destined to form a part of the spinal cord, consists of two sets, one of which runs in the anterior, the other in the posterior division of the crus, the one standing in a certain relation to consciousness, the other forming a part of certain reflex mechanisms.

The exact position occupied by the fasciculi that represent the cerebral

nerves in the crus cerebri cannot at the present day be defined in the mosaic-work of the cross-section preparations, and the only point of the truth of which it is possible to satisfy one's self, is that inasmuch as it is certain that the collective fibres of the basis cruris of one side decussate with those of the opposite side, and that this decussation must take place in this region between the fibræ rectæ and the raphe, the position of the fasciculi in question *before their entrance into the raphe* must be in the innermost region of the anterior division of the pons, *i. e.*, the anterior longitudinal fasciculi of the basis cruris, and in the corresponding part of the anterior pyramids, and indeed that such is probably their position from the period of their first association with the crus cerebri (*v.* p. 686, ansa peduncularis).

On the other hand, inasmuch as the fibres concerned in the production of reflex action cannot be supposed to undergo decussation invariably, we are deprived, in the localization of the fasciculi associated with the cerebral nerves in the midst of the posterior division of the pons and oblongata, even of the assistance which the certainty of the occurrence of this process previously afforded us, and the assumption of Schroeder v. d. Kolk, that such fasciculi occupy the district lying between the raphe and the hypoglossal nerve, cannot be proved to be true by following up the course of the tracts involved, though it finds some support in the undeniable fact that the dimensions of this district gradually become smaller, farther down. Better, however, than the *course* of these crural fasciculi toward the points where they terminate in the central tubular gray matter, can we determine these points of termination themselves, for they are characterized by being at the same time the points of origin of the cerebral nerves.

A large number of these so-called nuclei of the nerves (for the description of whose relation to the special nerve-roots we are indebted to Stilling) lie in the *gray matter which forms the floor* of the 4th ventricle, and indeed the prominences on the surface to which these nuclei give rise and the consequent furrows between them divide this floor into well-defined districts. Receiving its rhomboid form from the convergence of the *processus cerebelli ad cerebrum* above and the convergence of the *funiculi graciles* below, the 4th ventricle is divided by the *median furrow* of the calamus into two symmetrical lateral halves, and by the striæ medullares (or, when they are wanting, by an imaginary line uniting the two nervi acustici) into an upper and a lower half.

At the upper extremity of the floor of the 4th ventricle, exterior to the eminentiæ teretes (formations which were present even in the region of the aqueductus), is a depression, the *fossa cœrulea*, which forms the extremity of a sharp angle between the surface of the floor and its lateral wall, the epithelial investment of which depression gives a bluish tint to the dark-colored cells of the substantia ferruginea which lie beneath (figs. 273 and 275 F_1 5), in accordance with the laws that regulate refraction in slightly opaque media. About 6 mm. superiorly to the striæ medullares, *i. e.*, in the region where the inner surface of the processus cerebelli ad cerebrum is traversed by fasciculi belonging to the inner division of the pedunculus cerebelli (fig. 278 H'), lies the upper end of a district of the gray floor, *the inner nucleus of the auditory nerve* (*Clarke*), which has a rhomboid form, being limited inwardly by a furrow bent in an obtuse angle. It may be seen in cross-section at fig. 277 at 8. Stilling recognized the true character of the upper and larger portion of this district, triangular in shape, while he mistook its lower portion, which lies in the domains of the inferior half of the ventricle, for a *nucleus* of the *glosso-pharyngeal* nerve. The broadest part of this rhomboid district, which occurs at the middle of its length, cor-

responds to the position of the striæ medullares of the auditory nerve. To the inner side of the nucleus of the auditorius, above the region of the striæ, the motor column of the gray substance is represented by an oval-shaped elevation, the common nucleus of the *nervi facialis et abducens* (*Stilling*, *Clarke*) (fig. 277 near *G*).

The sulcus that lies between the upper half of the rhomb-shaped auditory nucleus and the last-mentioned oval elevation is not seldom made still more conspicuous by the occurrence of a number of *ascending striæ medullares* (J. Engels), which run parallel to the course of the sulcus, from the inner extremity of the striæ medullares transversæ upwards and outwards. They are in reality the *prolongation* of certain roots of the auditory nerve that form a part of the pedunculus cerebelli of the *opposite side*, or in other words they constitute the *superficial* fasciculi of origin of the auditory nerve from the *opposite hemisphere of the cerebellum.* Very often only the innermost fasciculus of the *ascending striæ medullares* is visible, and it might with great propriety receive again the designation chosen for it by *Bergmann*, of *conductor sonorus*, now that it is no longer regarded as an *inconstant* posterior root of the 5th pair, as Stilling considered it. That the striæ medullares are not seen in animals, does not signify that the fibres which compose them are really wanting, but only that they remain as naked axis-cylinders, *i. e.*, without medullary sheaths, and therefore invisible. Whether their medullary sheaths become developed or not, depends upon the degree of development of the respective brains themselves, which explains the fact that they are wanting in the brains of new-born Children, and especially constant, on the contrary, in those of Adults, as J. Engels has stated. It is for the same reason that the basis cruris cerebri of new-born Children appears gray instead of white. A closer study of this matter of the development of the white medullary nerve-sheaths of the Infant, appearing as they do at different periods in the different regions of the encephalon, would be attended with important results.

In the inferior half of the 4th ventricle, on each side, wedged in between the median elevation which is principally caused by the *nucleus* of the *hypoglossus*, a motor nerve, and that caused by Clarke's *inner nucleus of the auditorius*, lies the common nucleus of the *vagus and accessorius* (*Stilling*, *Clarke*), the nucleus of origin of a system of the so-called *median, lateral system of mixed nerves* (Deiters). Inasmuch as this nucleus sinks inwards below the surface at the upper end of the calamus scriptorius, between the nucleus of the auditory nerve and Stilling's nucleus of the hypoglossus (fig. 280 X^1, between the lateral and median elevations), it appears externally in the form of a triangle with one of its points directed upwards, and conversely the district occupied by the nucleus of the hypoglossus appears also in the form of a triangle, but with its point downwards, because this latter nucleus becomes gradually concealed by that of the vagus and accessorius, which is at first behind the former, but which becomes constantly more prominent, at the same time approaching the median line (figs. 280 and 281). The changes in the conformation of these parts are the cause of the gradual deepening of the ventricle, and the formation of the central canal. The nucleus of the vagus appears on the surface as a bare mass of gray substance, Arnold's *ala cinerea*, covered by its ependyma alone. The nucleus of the *hypoglossus*, on the contrary, does not lie exposed upon the surface, but is covered over by bundles of medullated fibres (fig. 280, X^4), by virtue of whose white color it is easily to be distinguished from the ala cinerea, and which are in fact fibres belonging to the roots of the vagus and accessorius nerves. The nucleus of the hypoglossus is moreover still

further covered by the mass of gray substance (*Clarke's* eminentia teres) from which these last-mentioned fibres spring, so that, strictly speaking, the median elevation of the ventricle should not be designated as the nucleus of the hypoglossus, as Stilling describes it, but rather as marking the *region* of that nucleus. The common nuclei of the vagus and accessorius of the two sides are connected together inferiorly by the commissure of the *obex* (Clarke, Deiters) (fig. 281, *Ob.*), the whole having a horseshoe-like form. The bundles of fibres from this commissure give especial prominence to the outer borders of the inferior halves of these nuclei, and the commissure itself sometimes (in the lower animals more constantly than in Man) lies within the limits of the open ventricle.

The obex is concentric with the *tæniolæ* which proceed from the substance of the funiculus gracilis, and which form the line of attachment of the embryonic roof of the 4th ventricle. The subsequent cover of the ventricle, attached along this line, and embracing the nucleus of the auditorius, divides from the rest of the ventricle two lateral diverticula, which, according to *Reichert*, are analogous to the lateral ventricles of the cerebrum.

In the 4th ventricle of the other Mammals (apart from the Apes), the regions of origin of the facial and hypoglossal nerves are much more easily recognizable as the representatives of the median motor column of *Lenhossek* than in Man, for the reason that in the lower animals the striæ medullares are wanting, and the nuclei of the auditory nerve further removed from the median line. The point of the calamus scriptorius is also wanting to the flattened, shallow 4th ventricle of the same animals, for while the ala cinerea is very slightly developed, the lower extremity of the nucleus hypoglossi remains quite broad, and is bordered below by the transversely-disposed, arched fibres of the obex.

The posterior division of the pons encloses, below the level of its greatest convexity, *i. e.*, below the level that is marked posteriorly by the completion of the disengagement of the processus cerebelli ad cerebrum from the lemniscus by which it had been covered, and anteriorly by the emergence of the 5th cerebral nerve from among the fibræ transversæ of the pons, the nuclei of origin of the 5th, 6th, 7th, and 8th * pairs of cerebral nerves which follow successively one upon the other.

The uppermost of these nuclei, the nucleus superior nervi trigemini of *Stilling*, gives rise to the *smaller main root of the 5th pair*. This nucleus lies in the lateral region of the motor district of the posterior division of the pons, in front of the ascending roots of the sensory division of the 5th nerve, to the inner side of the main root of that nerve at the level of its exit, and behind the stratum lemnisci, and exhibits on cross-section preparations an oblong surface displaying large (60–75 μ by 18–21 μ), well-defined, multipolar nerve-cells (fig. 275 right-hand side, fig. 276 left-hand side, *5m*). This nucleus is 3 mm. in height, its transverse diameter is 1.5 mm., its anterolateral diameter somewhat more than 1.5 mm. Its inferior extremity consists of a rounded mass only 0.8 mm. in thickness, which is separated from the main body by a slight interval.

This nucleus stands in connection, to all appearance, solely with the fibres of the inner, smaller root of the 5th pair, which are directed obliquely forwards and upwards, and which therefore appear on surfaces obtained by cross-sections as short, obliquely-directed longitudinal lines, between which the long processes of the nerve-cells are often to be followed for some little distance.

As to the question of the connection between the nucleus under consideration and the basis cruris cerebri, it can only be said in a general way, that in this region great numbers of fibres pass as fibræ rectæ of the raphe,

* The nuclei are numbered according to the method of Soemmering.—TRANS.

from the anterior into the posterior division of the pons, and, moreover, that they enter into connection within the raphe, with elongated, irregularly-disposed nerve-cells, which are of the same size with the cells of the nucleus itself, and must in fact be regarded as essentially a part of the latter. A similar disposition of the nerve-cells occurs in the region of origin of the hypoglossal nerve. In order to reach the nucleus of the motor root of the 5th nerve, these fibræ rectæ must pass into fibræ arcuatæ, of which they must necessarily form the posterior division. The tendency shown by many of the fibræ arcuatæ to turn their inner extremities forwards, speaks in favor of the correctness of this supposition.

Fig. 276.

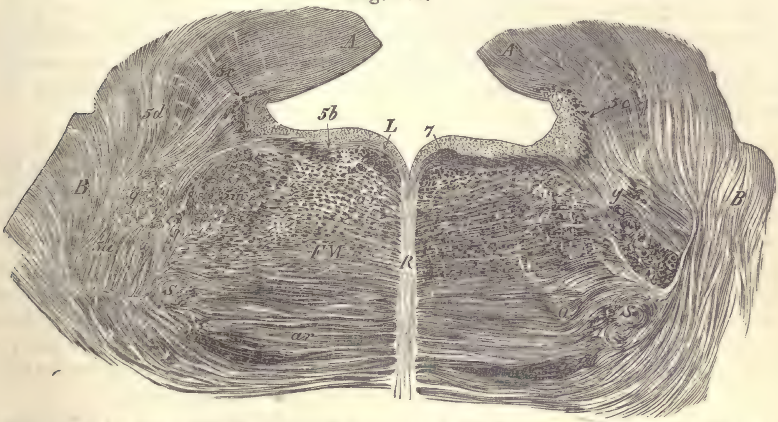

Fig. 276. *Transparent cross-section from the Human pons Varolii at the level of the origin of the greater root of the fifth pair. The plane represented in the right half of the section lies somewhat lower than that represented in the left half.* *A*, the processus cerebelli ad cerebrum; *L*, the posterior longitudinal fasciculus, lying just beneath the gray floor of the 4th ventricle, in the left half of the section capped by fibres from the raphe on their way to join the 5th nerve; 7, group of fibres belonging to the root of the facial nerve, lying behind the posterior longitudinal fasciculus, in connection, to the inner side, with fibræ rectæ of the raphe, and in close apposition to certain descending fibres of the root of the 5th nerve; *B*, the processus cerebelli ad pontem; *FM*, the motor district of the posterior division of the pons; *ar*, fibræ arcuatæ; *R*, the raphe; *S*, the region occupied by the fibres of the inferior lamina of the lemniscus after they have turned and taken a downward course (pes lemnisci); *g*, the gelatinous substance from which the 5th nerve in part arises; 5*a*, the greater main root of the 5th nerve; 5*b*, inner portion of the descending roots of the 5th nerve; 5*d*, roots of the 5th nerve from the cerebellum; 5*m*, nucleus of origin of the smaller main root of the 5th nerve; *Q*, cross-section of the ascending root of the 5th nerve, close to the outer side of which lie bundles of fibres belonging to the main root of the same nerve, on the way to the point of their emergence; *O*, neighborhood of the superior olivary body.

Nothing more definite, certainly, than the above can be said in explanation of the course of the nerve tracts, by means of which the superior nucleus of the 5th nerve is brought under reflex influences. Clarke was the first to call attention to a connection of this nature between this, the motor nucleus, and the sensory nucleus of the 5th nerve, and one is certainly tempted to recognize in the relative position of these parts the essential features of the structure of the spinal cord, the nucleus of origin of the greater sensory root of the nerve in question being the representative of the caput cornu superioris, while the superior nucleus might stand for the anterior cornu, or rather for its processus lateralis.

In truth, however, *Clarke* did not discover any such connection.

The region he describes as being its seat does not extend so high as to include the genuine nucleus of the motor root of the 5th nerve, and that nucleus which he described as standing thus in connection with the gelatinous substance is not a nucleus of the 5th nerve, but is the inferior nucleus of the facial nerve. The lower extremity of the real nucleus of the motor root of the 5th nerve, which I have found to be a small, distinct group of cells, often lying some little distance behind the inferior nucleus of the facialis, he does not describe as taking part in this connection. On the other hand, it is very possible that a reflex mechanism of this kind is established by the aid of nerve-tracts that originate in others of the manifold nuclei of origin of the 5th pair. The task of referring this nerve to its proper place in the structural type of the spinal cord, and of discovering the analogy between its mode of origin and that of the posterior spinal nerves, has not yet been performed with the accuracy that the importance of the subject demands.

The history of trismus certainly shows us that the connections of the nucleus of the motor root of the 5th nerve embrace the sensory tracts of the spinal cord, and it is therefore highly probable that a certain portion of the fibræ arcuatæ of the region under consideration, although they cannot be seen to join tracts that run downwards into the cord, will nevertheless be finally discovered to be in connection with its posterior columns. It is possible that the large, irregularly-disposed nerve-cells of the motor district of the oblongata, which at the region in question are somewhat more numerous than at a higher level, are to be regarded as outlying elements of the superior nucleus of the 5th nerve, and as serving to place the latter in connection with the posterior columns, by way of the fibræ arcuatæ.

The complicated mode of origin of the external greater sensory root of the 5th nerve will be made most easy of comprehension if the primary roots, by whose confluence the main root is formed, be studied, in respect to the manner of their origin, under four headings:—

1. *Roots of the 5th nerve which have their origin in collections of cells that lie within, or not far from the region occupied by the main root of the nerve.*—The collection of cells that gives origin to these tracts, which are of considerable dimensions, appears in longitudinal sections to the outer side of, and closely apposed to, the nucleus of the motor part of the 5th nerve, having itself a semi-lunar form. In the Human brain it has a height of 4.4 mm., and measures 1.2 mm. in its transverse, 2.8 mm. in its antero-posterior diameter. It is made up of small clusters of cells which are separated from one another by the delicate bundles of fibres that originate in the nerve-cells (fig. 276 *g*, 5*a*) and weave themselves into a network around them. The basement material of these clusters is finely-granular connective substance; their nerve-cells are for the most part 10–24 μ in length, and 6–9 in thickness. *Stilling* very properly regards the whole formation as a prolongation of the gelatinous formation, which extends downwards without interruption, still enclosed in the ascending root of the 5th nerve, to the caput cornu posterioris of the cord.

Certain of the innermost clusters of this nuclear mass, which lie more in the neighborhood of the nucleus of the motor root of the 5th nerve, contain elements of a larger size, 39 μ in length by 12 μ in thickness, so that in passing from the motor nucleus to the outermost clusters of the mass which has just been under consideration, we find nerve-cells of the three sizes that characterize the elements of the cornu anterius, the collis, and the caput cornu posterioris, respectively.

2. *Roots of the 5th nerve that have their origin above the plane of the main root, i. e., descending roots.*—The descending roots of the 5th nerve are of three orders:—

The outer of them (figs. 272 *V*, 273, 274, 5, 275 and 276, 5*c*) springs from large bladder-shaped cells, which extend from the region of the superior corp. bigeminum to the region of exit of the 5th nerve itself, and which give rise also, as was described above, to the fibres that traverse the tegmentum cruris cerebri as the connecting tract of the 5th nerve (p. 708). This root descends along the outer side of the central, tubular gray matter of the aqueductus, and passes onward through the region of the pons, in the mean time constantly increasing in bulk, and buried in the lateral region of the gray floor of the ventricle that lies along the inner surface of the processus cerebelli ad cerebrum. It presents on cross-sections a semi-lunar surface, which *Stilling* and *Deiters* took for an ascending trochlearis-root, and along its inner border lie, through a large part of its course, the clusters of cells from which the fibres of the root spring, so disposed as to remind one of grape-clusters. These cells are distinguished from those of the substantia ferruginea by the roundness of their form, and by their containing no pigment (p. 705).

The fibres of the middle division of the descending roots of the 5th nerve spring from the cells of the substantia ferruginea.

This elongated collection of pigmented, spindle-shaped nerve-cells (60 μ in length by 20–30 μ in thickness), which give its dark color to the locus cœruleus of the 4th ventricle, lies with its superior extremity in the lower half of the inferior corp. bigeminum, extends downwards for a distance of more than a centimetre to just above the region occupied by the main root of the motor part of the 5th nerve, lying all the time to the inner side of the *outer* of the descending roots (figs. 273, 274, 5, 275, *F*). Scattered cells belonging to this formation extend, however, into the lateral regions of the posterior division of the pons, appearing as large, deeply-pigmented elements, which lie with their long axes perpendicular to the gray floor of the ventricle, and standing in connection with nerve-fibres disposed in the same manner. These cells perhaps send connecting fibres to that division also of the descending roots which is next to be described. Similar dark-colored cells lie scattered in the roof of the 4th ventricle, to the inner side of the processus cerebelli ad cerebrum (substantia ferruginea superior). In the brain of Children and in that of the lower Mammals these cells, as well as those of the substantia nigra of Soemmering, are void of pigment, which, indeed, is always wanting to many of the individual elements of the formation in question.

The fibres to which the substantia ferruginea gives rise form a layer, 0.8 mm. in thickness, beneath the floor of the ventricle, run obliquely inwards, passing over the surface of or traversing the posterior longitudinal fasciculus, partly directly, partly obliquely, after interweaving themselves among its fibres, and finally run across the median line, thereby decussating, either in the region between the two post. longit. fascic. or anteriorly to them, with the corresponding fibres of the other side, at acute angles, after the manner of commissural fibres. During the decussation they describe curves with their convexities upwards. Having crossed the median line, these fibres direct their course outwards, passing partly through, partly in front of, the other posterior longitud. fascic., and finally bend forwards to join the current of fibres that make up the greater root of the 5th nerve, as the middle division of the chain of fasciculi that form a border for the floor of the ventricle (figs. 275, 276, 5*b*).

The posterior longitudinal fasciculus which is thus traversed by these systems of fibres, and still more the region which lies just in front of it, is very rich in nerve-cells that extend as far as the border of the posterior division of the pons. A few of these cells are of large size; the greater number are quite small. The middle division of the descending 5th nerve-roots seem to me to stand in connection with the larger cells.

The inner division of the descending roots of the 5th nerve is in all probability derived from the longitudinal fasciculi of the anterior division of the pons (the pes cruris cerebri), being composed of fibres which pass thence, under the form of fibræ rectæ of the raphe, into the posterior division of the pons. After decussating at acute angles with those of the other side, these fibres turn outwards and pass on, some in front of the post. longitud. fascic., some through, and some behind the same, to join the 5th nerve as the innermost division of the fibres that border on the floor of the ventricle, taking a position between the post. longitud. fascic. and the middle division of the descending roots of the nerve (fig. 275, right-hand side *L*, fig. 276, left-hand side *RL*). The fibres of the middle division of the descending roots, which run transversely across the raphe, and those of the inner division, that run longitudinally along the raphe, do not become interwoven with each other, but to all appearance the first-mentioned set arch over the last-mentioned. The fibres of the inner division of the descending roots enter into connection with the collections of small nerve-cells that lie before and behind the posterior longitud. fascic.

Stilling referred the origin of the two last-mentioned divisions of the roots of the 5th nerve simply to the gray substance forming the floor of the ventricle. I myself had previously considered them as made up of a group of fibres that pass beneath the thalamus opticus, at a level still higher than that represented at fig. 271, to attach themselves to the outer side of the posterior longitudinal fasciculus, and descend in its company. Inasmuch as these bundles of fibres run downwards between the external division of the descending roots of the 5th nerve and the poster. longitud. fascic., the very region whence a group of fibres of considerable size proceeds to join the greater root of the 5th nerve, I felt obliged to regard them as a part of this group. Having traced out subsequently, however, the course of the fibres from the substantia ferruginea, and having discovered how they cross the median line, and run along under the gray substance forming the floor of the ventricle on the opposite side, I see that the collection of fibres mentioned, lying to the outer side of the poster. longit. fascic., in the latero-posterior part of the tegmentum, although traversed and surrounded by the genuine descending root-fibres, probably do not themselves become a part of the 5th nerve.

3. *A root of the 5th nerve which has its origin below the region occupied by the main root. Ascending root.* On cross-sections from the lower part of the pons and the oblongata, as far down as to the lower extremity of the latter, there is to be seen, to the outer side of the region occupied by the projection-system fibres of the tegmentum, and to the inner side of the cerebellar processes, *i. e.*, at a point exactly corresponding to that occupied above by the central extremity of the main root of the 5th nerve (fig. 276, *G*, *Q*), a densely packed group of transversely cut fasciculi, whose upper extremities must, of course, lie at the point of origin of the root mentioned (figs. 277, 278, 279, 280, 281 *S*, *G*). The surface exhibited by cross-sections of this group of fasciculi has the form of a crescent, so disposed that its concavity is directed backwards, and enclosed within the latter lies a quantity of gray substance peopled with nerve-cells, for the most part of small size, in which, at the lower extremity of the oblongata, the mass of fibres in question terminate after breaking up into delicate bundles, and around which at the same moment the lateral and posterior columns of the spinal cord close to-

gether and coalesce. From this point onward this gray substance receives the designation of the gelatinous substance, or caput, of the posterior cornu. In the lower half of the oblongata the bulk of this gelatinous substance becomes greatly increased, being inflated to the tuberculum cinereum Rolando, for the reason that in this region it gives rise to the greater part of the ascending root of the 5th nerve (figs. 284, 285 *G*). Certain larger nerve-cells, foreign to the formation of the gelatinous substance proper, in which, however, they lie embedded at different regions of the pons and oblongata, are in my opinion to be regarded as belonging principally to the fibræ arcuatæ, and in part to the nerve-roots, by which the gelatinous substance is traversed.

4. *Roots of the 5th nerve derived from the cerebellum.*—Under this head belong bundles of fibres that either traverse or encircle the processus cerebelli ad cerebrum, and that in all probability become associated with the nerve in question, an opinion already pronounced by *Stilling* (figs. 275, 276, 5 *d*).

It is certainly satisfactory to be able to trace anatomically such a variety of modes of origin for a nerve that is associated functionally with so many different regions of the periphery of the body. We must, however, content ourselves with the simple objective enumeration of these modes of origin, for we have as yet no sufficient groundwork for the construction of a theory as to their functional significance.

Below the region of origin of the 5th pair, the floor of the ventricle is divided, on either side, by a lateral furrow, into a median district, the region of origin of the 6th and 7th cerebral nerves, and a lateral district, the region of origin of the nervus auditorius, the 8th nerve (fig. 277, *G* and 8).

The nervus abducens (fig. 277, 6) springs from *Stilling's common nucleus of the nervi facialis et abducens* (fig. 277, left-hand side 7^1), a dense collection, 1.6 mm. in thickness, of slender, multipolar nerve-cells, averaging 45 μ in length and 15 μ in breadth.

This nucleus, according to Stilling and Schroeder v. d. Kolk, is connected by the hindermost set of the fibræ arcuatæ with the raphe. I have further satisfied myself, by following them up carefully, that even those fibræ rectæ of the raphe that run from the region of the nucleus obliquely downwards toward the oblongata, change the direction of their course at the level of the inferior edge of the pons, and bend back into the anterior pyramids, *i. e.*, the continuation of the basis cruris cerebri. The common nucleus of the abducens and facial nerves of one side probably stands therefore under the influence of the nuclei of origin of the basis cruris cerebri of the opposite side.

At a point about 1.4 mm. above the lower border of the pons, the roots of the abducens emerge from this nucleus in the form of fine, distinct fibres, which run parallel to the raphe as far as the edge of the posterior division of the pons, and make their way thence obliquely downwards to the well-known point of exit of the nerve at the inferior surface of the pons. The outermost fibres of the main root of the abducens, which spring from the nerve-cells in the anterior part of the nucleus, may be seen to curve inwards and forwards toward their destination. The inner fibres of the same root, however, do not appear to be in connection with the nerve-cells of the nucleus, but form a dense fibrous layer behind it, in which a few nerve-cells lie scattered. I have been able to convince myself, however, that these fibres really do proceed from the nucleus, but that they are so disposed as to describe almost a circle around it.

The fibres in connection with the abducens then, like those in the nucleus of the hypoglossus (fig. 281 *XII*), are wound together into the form of a

coil. The central ends of the coiled fibres are in both cases continuous with the fibræ rectæ of the raphe, or more immediately with the hindmost set of the fibræ arcuatæ, being originally derived of course from the crus cerebri. They then appear to embrace the anterior and outer surfaces of the nucleus, enter into connection with its nerve-cells, and are transmitted by them to the main root of the nerve, in such a manner that they complete the circle around the nucleus by enclosing its posterior and inner surfaces. The principal reason that the course of these fibres cannot be demonstrated in its continuity, on section-preparations, is that that extremity of each of the coiled fibres which is in connection with the fibræ rectæ belongs to a plane inferior to that which corresponds to the nerve-root extremity of the same fibre. In that plane, for example, which is presented by the right half of fig. 277, and which lies superiorly to that represented by the left

Fig. 277.

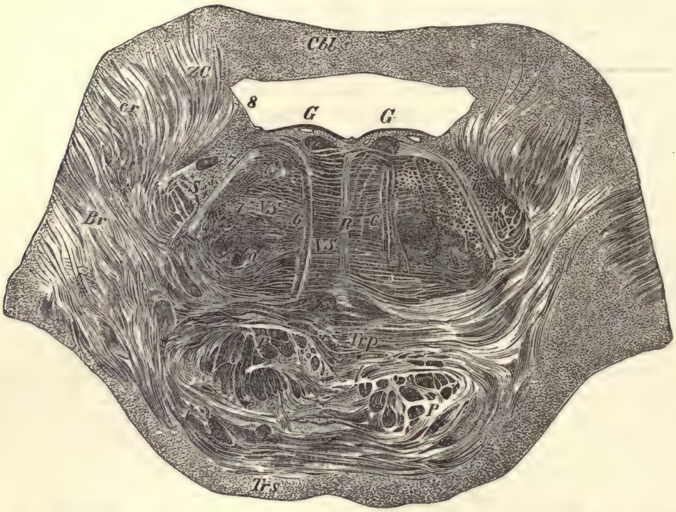

Fig. 277. *Transparent cross-section from the Human pons Varolii at the level of the origin of the nervi faciales and abducentes. The plane represented by the right half of the figure is somewhat higher than that represented by the left half.* *Cbl*, portion of the cerebellum constituting the roof of the 4th ventricle; *Zc*, inner division of the pedunculus cerebelli at its exit from the cerebellum; *Cr*, corpus restiforme (outer division of ditto) at its exit from the cerebellum; *R*, raphe of the posterior division of the pons; *Vs*, the motor district of the posterior division of the pons; *S*, the sensory district of same, containing the ascending root of the 5th pair; *O*, the superior olivary body; *Br*, the processus cerebelli ad pontem; *Trp*, the deep, *Trs*, the superficial stratum of its transverse fibres; *P*, the anterior longitudinal fasciculi of the pons; 7, the main root of the nervus facialis; *G*, genu nervi facialis; 7^1, the posterior (superior) nucleus of the nervus facialis, or common nucleus of the facialis and abducens;* 7^2, the anterior (inferior) nucleus of the nervus facialis; 6, the main root of the nervus abducens; 8, elevation on the floor of the 4th ventricle corresponding to the inner nucleus of the nervus auditorius.

half of the same figure, a portion of the root-fibres of the abducens is already visible, although nothing of the nucleus is to be seen.

Whether the roots of the abducens receive also, as *Schroeder v. d. Kolk*

* The 7 to the left of *VS* should be 7^2.—Translator's Note.

declared to be the case, a contingent of fibres from a nucleus as yet undiscovered which lies outside of, and superiorly to, that just described, must remain undecided. The same investigator makes the attractive suggestion that the fact that the central extremity of the main root of this nerve is directed away from the raphe, indicates that it is connected with its central innervating nervous centre by means of fibres that do not cross the median line, whereas the central extremity of the root of the oculo-motor, being directed towards the raphe, is evidently innervated by the nervous centre of the opposite side. To the existence of this arrangement he refers the simultaneous action of the rectus externus of the other side (comp. p. 709, co-ordination-mechanisms). If however the mode of the origin of the abducens is as I have described it, this suggestion loses its force for the case in hand, however true the general fact of the existence of such anatomical mechanisms for the production of special co-ordinated motions may be, to which I have already called the reader's attention in speaking of the fact that each half of the tegmentum cruris is derived in part from the ganglia of the same side, in part from those of the opposite side. I have however already laid down the general principle (p. 709) that no such mechanisms exist for the basis cruris, and the existence of the connections between the nucleus of the nervus abducens and the raphe seems to show that the course of the fibres sent to this nerve does not differ from that of the other fibres of the basis. Whether the innervation of the abducens by certain special centres of co-ordination (corpus quadrigeminum) takes place directly, or whether by means of fibres that cross the median line from the opposite side, must be determined by studying the history, in other parts of their course, of the tracts by which that nerve is connected with the centre in question. Certainly the interesting fact discovered by *Gudden* is worthy of mention in connection with the influence exercised upon the abducens by a distant nervous centre in the neighborhood of the origin of the nervus oculo-motorius, viz., that a flattened bundle of fibres passes transversely from the corp. bigeminum superius into the crus cerebri (tractus transversus pedunculi), which *Gudden* found to attain only to an imperfect degree of development when, in new-born animals, he rendered the retina incapable of performing its functions, and which therefore may be supposed to bear a certain functional relation to that organ. The fasciculus itself had been already noticed and correctly figured by *Inzani* and *Lemoigne.*

According to *Clarke* there are also certain delicate bundles of fibres belonging to the roots of the nervus abducens that curve round the nucleus of the facial nerve, after converging, pencil-like, from the eminentia teres, where they have their origin.

The roots of the *nervus facialis* originate in manifold ways, which we will again consider for the sake of clearness, under the following heads:—

1. *Roots of the nervus facialis that have their place of origin above the region occupied by the main root of the nerve. Descending roots.* They pass through the raphe from the basis cruris, as fibræ rectæ, cross the median line and run in curves with their convexities upward, arching over the common nucleus of the facial and abducent from above, without interruption, into the main root of the facial nerve (fig. 277, right-hand side, the light-colored bundles of fibres lying in front of the dark surface marked *G*). Because of the curves which they describe, it is impossible to trace these fibres actually into the root, except in sections passing through the very uppermost portion of the region of origin of the nerve in question, for any section made at a lower level cuts off the summit of the arch. There is also a certain set of descending fibres that run, not within the raphe, but across the

motor district of the tegmentum, and therefore across the path of the fibræ arcuatæ, on their way to the main root of the facial nerve (fig. 277, right-hand side, between *R* and 6). It is of course uncertain whether the fibres of this set have a common place of origin (the nucleus lenticularis, for example) with those first mentioned descending facialis roots that form the fibræ rectæ of the raphe.

2. *Roots of the nervus facialis that have their origin within the region occupied by the main root of the nerve.* They spring (*Deiters* holds a contrary opinion) from the common nucleus of the facialis and abducens, or rather from its upper half, for it is doubtful whether in its lower half this nucleus has any connection with the facial nerve. As far as they are in connection, however, the root fibres are to be seen emerging from the region of the nucleus, occupying a space exactly corresponding to the latter in breadth, so that there can be no doubt of their relation therewith (fig. 277, left-hand side).

3. *Roots of the nervus facialis which have their origin below the plane occupied by the main root of the nerve. Ascending roots.—Dean* and *Deiters* described the course of these roots independently of each other, and both correctly, at least so far as one can judge from Deiters' unfinished description. *Clarke* too would have perfectly understood their relations, had it not been that he considered the superior olivary body to be their nucleus of origin, instead of the inferior nucleus of the facialis, which he had previously mistaken for the nucleus of the motor root of the 5th nerve.

Their real nucleus of origin is then the anterior (inferior) nucleus of the facialis, a mass of large, elongated, multipolar nerve-cells, 60 μ in length by 21 μ in thickness, that reaches inferiorly almost to the lower border of the pons, and extends upwards nearly to the level of the region occupied by the common nucleus of the facialis and abducens, a distance of about 3.5 mm.; its transverse diameter measures 1.6 mm., its antero-posterior diameter 2.4 mm.

This nucleus lies close to the outer side of the superior olivary body, and in Man is sharply defined (fig. 277, left-hand side, 7) by a system of fibres that are coiled around it, the central extremities of which undoubtedly serve to attach the nucleus to the raphe and thereby to the *crus cerebri.*

In animals the nucleus is less sharply defined, because the elements of the coil are pressed apart, and their disposition obscured, by the introduction of a large quantity of connective substance (as was the case with the glomeruli olfactorii) (fig. 278, 7). The peripheral ends of these coiled fibres appear as fine, distinct lines, that curve outwards and backwards toward the gray matter forming the floor of the 4th ventricle, where they gather themselves to a compact fasciculus which makes a knee-shaped bend upwards (Deiters). This fasciculus (the genu nervi facialis) appears on cross-sections, throughout the entire length of its course, a distance of 5 mm., as a dark, sharply defined spot, lying behind, and to the inner side of, the root of the abducent nerve and its nucleus (fig. 277, left-hand side, *G*). It seems in fact to be actually separated by these two last-mentioned structures from the *main root of the facial nerve* for which it is destined, which is to be accounted for by the fact that the genu is connected with the nerve itself by an arch of fibres, the summit of which lies superiorly to the plane of the sections referred to, which pass through its two branches. In the curve of this arch lies the common nucleus of the facialis and abducens. Leaving the genu to pass out with the main root of the nerve, this root then describes again, in the reverse direction, the curve described by the fibres which connect together the nucleus and the genu, the two curves being thus

parallel with each other, but separated by an interval of 5 mm. (fig. 277, *G*, 7, right-hand side). Inasmuch as the main root of the facial nerve occupies a space in the pons which measures from above downwards about 2 mm., it is plain that its most inferior bundle of fibres must appear, in a series of transverse sections, opposite to the genu (fig. 277, left-hand side).

This set of fibres that forms the ascending root of the facialis is then not in connection with the nucleus of the abducens, but curves round the outside of, and avoids, both the nucleus and the root of that nerve, by describing a course of the form of a *horseshoe* bent somewhat out of shape. The two branches of this horseshoe lie in the pons, *the one above the other*, and parallel with each other. The *lower branch* consists of the fibres that run inwards and backwards, from the anterior (inferior) nucleus of the nerve to its genu (fig. 278, 7^1); the *upper branch* is made up of the fibres that run from the upper extremity of the genu, outwards and forwards, toward the point of emergence of the nerve (fig. 277, right-hand side). The *genu* itself forms the curved end of the horseshoe, *connecting together* its two branches. This central connecting piece of the horseshoe is however at the same time bent inwards, in the direction of a line perpendicular to the surface of the horseshoe, in order that it may embrace the inner surface of the facialis and abducens; and further, the *upper branch* is bent upwards at one point, in the direction of the plane of the surface of the horseshoe, in order that it may arch over the nucleus mentioned.

The uppermost of the fibres that bend from the superior extremity of the knee into the main root of the facial nerve, arch upwards so high as to make their appearance in the region of origin of the 5th nerve (fig. 276, 7), which accounts for Stilling's having regarded the genu nervi fac. as a constant posterior root of the 5th nerve, and for his having designated the *nucleus of the facial nerve* as *the inferior nucleus of the trigeminus.*

The main root of the nervus auditorius comes into existence at about the level of the nucleus of origin of the ascending root of the nervus facialis (fig. 278, 8), and stands in connection, within the region of the pons, with the following masses of gray matter, four in number:—

1. *The inner nucleus of the nervus auditorius* (*Stilling* and *Clarke*).—This nucleus may be divided for purposes of description into three parts, lying one above the other. In the region of the uppermost of these divisions, the nucleus lies to the outer side of the elevation corresponding to the superior nucleus of the facial nerve (fig. 277, 8); in that of the *middle* division, which lies pretty nearly at the level of the striæ medullares, it occupies the entire breadth of the floor of the ventricle (fig. 278, *VIII*); in that of the lowest division, it lies to the outer side of the region of origin of the glossopharyngeus and the common nucleus of the vagus and accessorius (fig. 280, 8). This nucleus is traversed, beneath the gray substance forming the floor of the ventricle, by great numbers of densely disposed, fine bundles of fibres, that run for the most part in the direction from the cerebellum toward the raphe, and scattered among them lie nerve-cells 30–45 μ in length by 12–15 in breadth.

2. The *external nucleus of the nervus auditorius* (*Clarke*, *Dean*), occupies that trapezoid-shaped district of the inner division of the pedunculus cerebelli that is in immediate apposition with the inner nucleus of the nerve in question (fig. 278, left-hand side *H*, right-hand side behind 8^4, fig. 280, *SFC*). It has a common posterior and a common anterior boundary with this latter nucleus, and impinges externally on the corpus restiforme pedunculi cerebelli. The external nucleus is, in its inner half, traversed by

densely disposed bundles of fibres belonging to the inner division of the pedunculus cerebelli. Exteriorly to these it consists almost exclusively of gray substance (fig. 278), and in this portion of it lie great numbers of multipolar, elongated nerve-cells, 60–100 μ in length, by 15–21 in thickness.

Fig. 278.

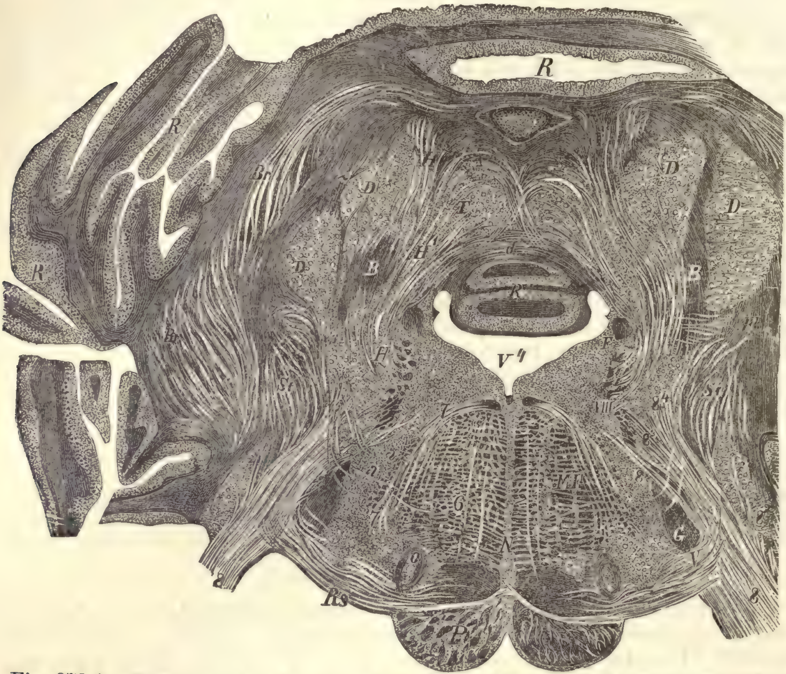

Fig. 278.* *Transparent cross-section from the cerebellum and the upper extremity of the oblongata of Cercocebus cinomolgus, showing the nervus auditorius at its origin. The plane represented by the right half of the figure, lies in reality somewhat inferiorly to that represented by the left half.* V^4, the 4th ventricle; *RRR*, the cortex of the left hemisphere, and of the superior and inferior vermiform processes of the cerebellum; *VIII*, the inner nucleus of the nervus auditorius; *N*, the raphe; *P*, the anterior pyramid; *MF*, the motor district of the posterior division of the oblongata; *G V*, the gelatinous substance, with the ascending root of the 5th nerve; *a*, fibræ arcuatæ standing in connection with the inner division of the pedunculus cerebelli; *H*, the inner division of the pedunculus cerebelli; *St*, the outer division of the pedunc. cerebel. (between the two divisions lies a collection of large nerve-cells); *Br*, the processus cerebelli ad pontem; *Rs*, corpus rhomboideum (trapezoides); *O*, superior olivary body; 7, inferior nucleus of the facial nerve lying to the outer side of *O*, from which emerge the roots of the facial nerve 7^1, which finally lose themselves in the section of the genu nervi facialis, that lies close to the gray substance forming the floor of the ventricle; 6, nervus abducens; 8, nervus auditorius, made up of fibres: (8^1), from its inner nucleus which lies near the floor of the ventricle of the fibres; (8^2), from *Stilling's* anterior nucleus of the same nerve, of fibres from the inner division of the pedunculus cerebelli (8^3), and from its outer division (8^4); *D*, the nucleus dentatus of the cerebellum; *T*, *Stilling's* nucleus tegmenti of the cerebellum; *B*, the medullary substance belonging to the inner division of the pedunculus cerebelli from the hemisphere of the opposite side; H^2, ditto from the hemisphere of the same side above the corpus restiforme, both in cross-section and in longitudinal section, its fibres running in the latter case in a transverse direction.

* The 7, a little below and to the left of V^4, should be 7^1. The 8, immediately on the right of *MF*, should also be 8^1.

3. The *anterior nucleus* of the *nervus auditorius* (fig. 278, 8^2), a wedge-shaped mass of cells inserted between the auditory nerve, the corpus restiforme, and the medullary substance of the flocculus, presents on cross-section, in the Human brain, a triangular surface 3 mm. in length and 2 mm. in breadth. It is made up of closely-packed, bladder-shaped nerve-cells, furnished with but few processes, resembling the component elements of the spinal ganglia in form, but not in point of size, as the former are much the smaller of the two, and are enveloped like these each in a delicate membrane, and contain small nuclei.

4. *Certain nerve-cells lying in the main root of the nervus auditorius*, occurring singly and in clusters throughout the central course of the latter. They are present in such numbers at the point of its emergence, at the anterior border of the pons, that they inflate the nerve to a ganglion-like body, and they further lie embedded in the external portion of the main root that passes to the outer side of the pedunculus cerebelli. Their size, which is generally very considerable, their elongated form, the great number of their processes, and the presence of enveloping membrane, forbid us to regard them as belonging to the same formation with the anterior nucleus, as *Stilling* and *Clarke* have described them.

As to the nerve tracts that stand in connection with these various nuclei, we must distinguish, as in all other cases, between the fibres that have their origin in these nuclei, and those that terminate in them, having descended to them from nervous centres that occupy still more central positions.

There are as yet no grounds that justify us in drawing a morphological parallel between the auditory nerve and the *olfactory lobe* and *optic nerve*, with which one is tempted to classify it, on account of the peculiar and important function of the organ of sense with which it is in connection. The considerations that caused us to regard the olfactory lobe and the retina as having the same morphological significance with the cortex cerebri, do not hold good as regards the labyrinth of the ear, the organ of Corti. While the medullary substance belonging to the olfactory lobe and the retina (*i. e.* the optic nerve) penetrates, as we have seen, into the very same terminal ganglia with the medullary substance of the cortex cerebri, and terminates there in exactly the same manner with the latter, which represents the superior member of the projection-system, the auditory nerve, on the other hand, does not make its way into any one of these ganglia, but terminates in the central tubular gray matter, which is not in immediate connection with the cerebral lobes. The fact of its immediate entrance into this gray substance and the nature of its connection therewith are manifestly points which the nervus auditorius has in common with the nerve-roots in general, that represent the inferior member of the projection-system. This does not, however, justify us in placing the auditory nerve, in respect to the details of its further course, unreservedly in the same category with the other nerves of the caudex cerebri, nor in referring it to a definite place in the structural type of the spinal cord. Deiters attempts this in seeking to show that all the above-mentioned nerves form, in virtue of their mutual relations, members of his lateral mixed system of nerves, the other members of the same system which, like the rest, are neither purely sensory nor purely motor in their character, being represented by the glosso-pharyngeal nerve and the vagus and spinal accessory. In making this attempt, he only revives the old notion held by *Galen*, *Fallopia*, and *Haller*, that the auditory nerve (portio mollis) forms with the facial nerve, morphologically speaking, a single nerve-root.

Deiters took this view of the significance of the nervus auditorius, under

the belief that the opinion already pronounced in general terms by *Foville*, and *Schroeder v. d. Kolk*, that the origin of the nervus auditorius is to be sought in the cerebellum, was an erroneous one. I desire, however, before entering into the details of the description, to express the decided opinion that its connection with the cerebellum (which is partly brought about by decussation) gives to the *nervus auditorius the right to be placed in a different category from other nerve-roots*, an opinion which is based on microscopic work done by me a number of years ago, and which *Clarke* and *Dean* have lately confirmed.

In accordance with the sequence which has been observed in the description of the relations of all the other nerves, I should speak next of the system of nerves which places the cerebral lobes, by way of the crus cerebri, in connection with the nuclei of origin of the nervus auditorius, a connecting system that, on physiological grounds, we should expect to find of as considerable dimensions as that leading to the retina, the optic nerve. Surprisingly enough, however, no such system of connecting fibres between the nervus auditorius and the crus cerebri is to be discovered.

It is true that on sections from the common region of origin of the auditory and facial nerves, we find an appearance that leads us to conclude with certainty that the entire posterior longitudinal fasciculus makes a sudden bend, and passes over into the nuclei of origin of the nervus auditorius (fig. 279, 8, *VIII*) which lie to its outer side, and I was originally induced thereby to attribute to the posterior longitudinal fasciculus the significance of an auditory-tract. Subsequent preparations, however, from the pons Varolii of the Dog, the coloring of which happened to be unusually successful, have enabled me to trace with more accuracy the facts of the case, and have convinced me that the posterior longitudinal fasciculus continues in fact to pass downwards to the anterior column of the spinal cord (*Stilling*), being traversed, however, by the systems of fibres on their way towards the auditory nerve in such profusion that it seems to be itself diverted from its course, and to pass over into the nucleus of the latter.

It is true that Stilling has succeeded in following the fibræ rectæ of the raphe into the external roots of the auditorius (striæ medullares), but it is certain that the greater number of them do not serve to establish any connection between this nerve and the crus cerebri, for they can be traced in the opposite direction across the median line, and, as fibræ arcuatæ, into the pedunculus cerebelli of the opposite side.

In the light of the foregoing statements it may be regarded as certain that no considerable *immediate* connection exists between the auditory nerve and the cerebral lobes, and we are obliged to conclude that a *mediate* connection, the presence of which in one form or another physiological considerations require us to admit, is established by way of the cerebellum.

Of all the connecting tracts that spring from the cerebellum, only the processus ad cerebrum, or the velum medullare anterius with the frenulum, can be thought of in this connection. One is tempted to regard the processus ad cerebrum as representing the connecting tract in question, on account of its dimensions, which are about the same as those of the optic nerve, and should that really be the case, the decussation of the two processes within the tegmentum might be regarded as forming an *acoustic chiasma*.

The fibres that by their confluence make up the nervus auditorius belong to the following systems, some of which have their origin in the nuclei already mentioned.

In the first place, however, an anterior main root, which traverses the pons anteriorly to the pedunculus cerebelli, is to be distinguished from a

posterior main root, the outermost fibres of which pass to the outer side of the same pedunculus, and to which the striæ medullares belong. The *anterior* main root occupies a space measuring 2 mm. in its upright diameter, and rather more than 1 mm. in its transverse diameter, between the corpus restiforme and the ascending root of the 5th nerve, and is made up of fibres that spring in part from nuclei of origin of the same, in part from nuclei of origin of the opposite side.

1. The fibres derived from the *opposite side* are the *innermost* of those composing the anterior main root. They have their origin, to all appearance, in the *inner auditory nucleus* of the *same side.* In fact, however, they only pass through this inner nucleus and the corresponding inner division of the pedunculus cerebelli, on their way from the raphe to the main root, and they are in reality derived from the inner division of the pedunculus cerebelli of the opposite side, and in respect to their course thence are divisible into two sets. One set run from the respective pedunculus cerebelli longitudinally through the inner nucleus of the auditory nerve, in the same direction with *Bergmann's* conductor sonorus, or, in other words, with the ascending striæ medullares of *J. Engels* (terminating, like them, at the inner extremities of the striæ medullares transversæ), some of them lying exposed on the surface under the form of the striæ medullares ascendentes just mentioned, some of them buried below the surface (in front of the *genu nervi facialis*). They all cross the median line, and pass through the inner auditory nucleus of the opposite side. They also traverse both posterior longitudinal fasciculi on their way.

Such being the course of this system of fibres, it is easy to see that the fasciculi H^1 in fig. 278, that traverse the posterior set of the series of cross-sections H, that occupy the inner division of the pedunculus cerebelli, must be directly continuous with the fasciculi 8^3 of the main root of the auditorius that are woven in among the *anterior* set of these cross-sections, and that they must traverse on their way the inner nucleus of the auditorius *VIII.* It is evidently impossible to trace the entire course of these fasciculi on any one section. One phase in their course is shown by fig. 279, 8,″ *VIII.*

The *second* set of the fibres from the pedunculus cerebelli pass directly forwards through the outer nucleus of the auditorius of the same side, but, without traversing the inner nucleus of that side, they continue their course under the form of fibræ arcuatæ (fig. 278 *a*), that run collectively in front of the posterior longitudinal fasciculus, as far as to the raphe. Here they turn toward the floor of the ventricle, and, crossing the median line, make their way through the posterior longitudinal fasciculus, passing onwards behind the latter through the inner nucleus of the auditorius. Together with the group of fibres first mentioned that run, after their decussation, transversely through the outer nucleus of the auditorius into the main root of the nerve, these last mentioned fibres, that traverse the same nucleus before their decussation, form there a right-angled, trellis-like formation, in the apertures of which are lodged the component fibres of the inner division of the pedunculus cerebelli, which are in the midst of their course downwards (figs. 278 *H*, 280 *SFC*). The innermost set of the fibres of the exterior main root traverse the ascending root of the 5th nerve, and the undermost of them, at their entrance into the main root, pass, not through the pedunculus cerebelli, but close to its anterior surface. *Stilling* considered the latter set of fibres to be the only ones concerned in the formation of this portion of the auditory nerve, referring their origin to the nucleus of the same side.

Those fibres of the anterior main root which do not cross from the opposite side are derived :

2. From the *outer nucleus* of the nerve in question (*Clarke*, *Dean*), of which the large cells form, to the outer side of the group of cross-sections referred to, a nuclear mass which for the most part is free from the admixture of foreign elements. The processes of these nerve-cells evidently pass over into the fibres of the root (fig. 278, 8^4). The course of these same fibres is prolonged in the opposite direction beyond the nerve-cells into the substance of the cerebellum, passing on their way, as I have satisfied myself by the study of preparations from the Human brain, through the processus cerebelli ad cerebrum, as well as to the outer side of it (*Clarke*, *Dean*) (fig. 278, left-hand side *B*).

3. From the *corpus restiforme* (fig. 278, *St*).

4. From the *anterior auditory nucleus* (*Stilling*), which again plays the part of a connecting link between the fibres of the root of the nerve and the medullary substance of the cerebellum (fig. 278, 8^2).

The *posterior* main root of the auditorius is formed by the confluence of:

5. The superficial system of fibres, the *striæ medullares*, which run over the surface of the inner nucleus of the nerve and the pedunculus cerebelli. They pass as fibræ arcuatæ, from the inner division of the pedunculus of the opposite side as far as to the raphe, then turn and run by way of the latter to the surface of the floor of the ventricle.

6. The *deep-seated* system of fibres, although, to be sure, they pass over the surface of the pedunculus cerebelli of the same side of the main root for which they are destined, do not appear on the surface of the floor of the ventricle, since, while conducting themselves on the side where they originate in the same manner with the fibres which form the later striæ medullares, they do not, within the raphe, run backwards as far as to the surface. The more posterior of the system of deep-rooted* fibres, inasmuch as they run backwards in the raphe nearly to the bottom of the median sulcus, traverse in the second part of their course the inner auditory nucleus in its entire breadth. The more anterior, however, which turn off from the raphe before reaching the gray substance that forms the floor of the ventricle, form, on the side corresponding to that of the emerging nerve, fibræ arcuatæ, which traverse the anterior corner of the inner nucleus, within the limits of which, close to the border of the pedunculus cerebelli, they turn and direct their further course backwards. Passing between the more posterior of the group of cross-sections that occupy the inner division of the pedunculus cerebelli, these fibres run toward the floor of the ventricle, and pass, with the rest of the fibres of the posterior main root of the auditorius, over the outer surface of the corpus restiforme (fig. 280, the bundles of fibres lying between *X* and *X′*, and those lying behind *SFC*).

Finally, another set of the fibres which form the posterior (exterior) main root pass through the corpus restiforme, as *Clarke* and *Dean* have shown, instead of to the outer side of it. This set probably consists of fibræ arcuatæ (Bogenbündel) from the inner division of the pedunculus cerebelli of the opposite side. Like the auditory nucleus itself, so the fibræ arcuatæ and root-fibres that are in connection with it are to be found as far down as in the region of origin of the vagus nerve (fig. 280 *VIII*).

All the numerous fibræ arcuatæ that are concerned in the formation of the auditory nerve, lie behind those fibræ transversæ of the posterior division of the pons that stand in connection with the superior olivary bodies.

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* The original text says "superficial fibres," but the context plainly shows it to be an oversight.

The large, scattered nerve-cells of the posterior division of the pons are moreover in connection with these fibræ arcuatæ; and if, as *Deiters* suggested, these cells are to be regarded as outlying elements of the motor nuclei of the facial, hypoglossal, vagus, and spinal-accessory nerves, then it may be that, in virtue of their relation to the auditory tracts, they serve to establish, within the limits of the posterior division of the caudex cerebri, a connection between the tracts belonging respectively to the sound-receiving and to the sound-producing organs, whereby the excitations of the one are reflected upon the other.

The fact that the perception of a sound is able to call out a reflex motion of the eyes in the direction whence the sound is supposed to have come, reveals perhaps the physiological significance of a connection of the kind just described between the auditory tract and the nervus abducens.

It is in the structure of the oblongata that we are first able to distinguish as a natural division the above-mentioned *intermediate system* of nerves, which can have been but artificially adapted by Deiters to the structure of the pons Varolii, a system which is really made up partly of sensory and partly of motor constituents. It embraces the 9th, 10th, and 11th cerebral nerves, whereas the 12th nerve has the position of an *anterior* (inner), and the ascending root of the 5th nerve that of a posterior (outer) nerve-root (figs. 280, 281, *X*, *XI*, *XII*, *S G*).

The structural type which underlies the mode of origin of the two last mentioned nerves finds expression again in the region of the spinal cord, in the distinction of the roots of the nerves into anterior and posterior, but the type of the *intermediate* system terminates with the formation of the last fibres of the root of the spinal-accessory. The modes of origin of the two members of this *intermediate* or *mixed lateral* system, the *glossopharyngeal* and the *vagus* and *spinal-accessory*, bear so much resemblance to each other that they may be described together.

The gray substance forming the floor of the ventricle, in which the greater number of the nuclei of origin of the nerves in question are embedded, presents on its surface, for a certain distance below the striæ medullares, a laterally disposed elevation, the inner nucleus of the auditorius with the fasciculi occupying the inner division of the pedunculus cerebelli (fig. 280, *VIII*, *S F C*). These nuclei disappear gradually and simultaneously as they approach the lower part of the ventricle, and the fasciculi of the pedunculus pass over into fibræ arcuatæ of the posterior division of the oblongata.

To the inner side of the auditory nucleus there lies, along the median line of the ventricle, an elevation that Clarke has lately designated as the *fasciculus* (eminentia) *teres* (fig. 280, X^4 to X), and with great propriety, for the nuclei of the hypoglossus do not at any point reach to the ependyma investing the floor of the ventricle. On the other hand, in the region of the ventricle as well as when lying in front of the central canal, these nuclei are covered over by the *eminentia teres* (fig. 281, the dark mass of substance behind XII^1 and XII^2), which is made up of small nerve-cells (21–30 μ by 6–9 μ) and a great number of nerve fibres. Besides its principal mass, the eminentia teres has to its inner side a spindle-shaped appendix, its *nucleus medianus*, lying close to the median line. It is made up of the same elements with the main body. The two masses, which are both to be regarded as nuclei of origin of the nerves of the intermediate system, are most fully developed immediately below the striæ medullares, and taper off toward the lower part of the ventricle, thus forming a club-shaped body.

On cross-section preparations another formation, known as the anterior projection (vordere Ecke) of the gray substance forming the floor of the ventricle, is to be distinguished from the auditory nucleus and the eminentia teres, between which two masses it wedges itself in. It contains, at the upper extremity of the oblongata, *Clarke's two nuclei of the glossopharyngeal nerve*, inconsiderable cell-clusters made up mostly of spindle-shaped elements 45 μ in length by 15 in thickness. The *outer* of them lies at the extremity of this anterior projection, the inner 1 mm. further inwards.

Lower down, this anterior projection of the gray floor of the ventricle becomes the seat of the *posterior* nucleus of the vagus (fig. 280 X^1), a mass in which *Clarke* again distinguishes an outer and an inner nucleus.

This nuclear mass, made up of spindle-shaped elements 30–45 μ in length by 12–15 μ in breadth, disposed with their long axis directed toward the point of origin of the main root, is the upper portion of the *common nucleus* of *the vagus* and *accessorius* of *Stilling*, and may be regarded, *taken together with Clarke's glossopharyngeal nuclei*, as forming the posterior column of origin (hintere Ursprungssaüle) of the *mixed lateral system*, the prolongation of which forms in the spinal cord the base of the *posterior cornu*. Limited at first to the anterior projection of the gray floor (fig. 280), this nucleus of origin of the vagus approaches nearer and nearer to the surface, the auditory nucleus and the eminentia teres becoming at the same time more and more reduced in size, and appears finally as the ala cinerea on the floor of the ventricle, where, having passed over into the nucleus of the spinal accessory, it lies laterally from (and behind) the central canal (fig. 281 XI^1). This common nucleus of the vagus and accessorius is surrounded by large numbers of highly pigmented nerve-cells, of about the same dimensions with its own, not very densely disposed, and has to its outer side, defined and bordered by fine fibrillæ coiled up in a peculiar manner, a cluster of spindle-shaped cells only 21–24 μ in length by 6 μ in thickness, that first makes its appearance just below the inferior extremity of the nucleus of the auditorius, and may be found to be in connection, after the closure of the central canal, with the commissural fibres of the obex. Its spindle-shaped cells are directed toward the point of origin of the root with which they are in connection.

Some distance anteriorly to the nucleus of the vagus and accessorius, surrounded by the longitudinal fasciculi of the posterior division of the oblongata, lies the *anterior* column of origin (vordere Ursprungssaüle) of the mixed lateral system (fig. 280, X^2), an oblong-shaped nucleus separated by an interval of 3 mm. from the ventricular gray substance. It is made up of multipolar nerve-cells 60 μ in length by 21 μ in thickness, and among them run the fibræ arcuatæ concerned in the formation of the posterior columns of the oblongata, with which their long processes evidently enter into connection. *Deiters* recognized the true nature of this nucleus, to judge from his indistinct mention of certain motor vagus roots, whereas *Clarke*, in consequence of his having misconceived the nature of the inferior facialis nucleus, looked upon this as a prolongation of the latter, *i. e.*, of his motor nucleus of the 5th nerve.

This nucleus is to be carefully distinguished from that of the lateral column of the oblongata, which lies farther backwards and outwards, and of which mention was made above in the course of the description of the cell-cluster formation.

This *anterior nucleus of origin* of the *mixed lateral system* takes, in the oblongata, the place of *processus lateralis* of the anterior column of the spinal cord. From this nucleus spring part of the upper, from the processus late-

ralis the lower, fibres of origin of the lateral system, *i. e.*, the nervus accessorius (fig. 284 *XI*).

In close apposition with the anterior border of the root of the 5th nerve lies an elongated collection of rather densely-packed, quite large spindle-shaped cells, disposed after the fashion of radii, that seem also to belong among the nuclei of origin of the system under consideration.

The nuclei of the lateral system are in connection with the *crus cerebri:* 1st, by means of fibræ rectæ of the raphe, that pass over into the system of fine fibres that run in curves through the *median nuclei* and the *eminentia teres*, toward the central extremity of the main root, and which are mentioned by *Deiters* as bordering, but not belonging to, the nucleus of the hypoglossal nerve (figs. 280, 281, $X^4 R$, $XI^3 R$). 2d, by means of those of the *fibræ arcuatæ* lying in the neighborhood of the ventricular gray substance, that pass from the raphe into the common nucleus of the vagus and accessorius (*Stilling*, *Schroeder*, *Clarke*, *Gerlach*). Two other fibrous tracts, that connect the *crus cerebri* with the *lateral intermediate system* of the oblongata, pass by a direct course into *the roots of the nerves concerned.* They will be the first to be mentioned in the enumeration of the *roots* of the *lateral mixed system.*

These are: 1. The *ascending common root of the nervi glossopharyngeus, vagus* and *accessorius*, the *solitary fasciculus*, recognized even by *Stilling* and *Lenhossek*, that in the region of the ventricle lies close to the inner border of the pedunculus cerebelli, further down close to the inner border of the posterior column (fig. 280, not specially designated, 281, *W*). The fibres that make up this fasciculus emerge from the raphe a short distance above the place of decussation of the anterior pyramids, within the region of origin of the accessorius roots (fig. 281). They are probably derived from the anterior pyramids, *i. e.*, from the basis cruris cerebri. In passing from the raphe, they form the second set of the fibræ arcuatæ (counting from behind forwards), and then become collected into the above-mentioned ascending root, which, after reaching the region of origin of the vagus, ceases to receive additional fibræ arcuatæ. This fasciculus contains, especially along its border, small nerve-cells (21–30 μ by 9 μ), through the agency of which it sends off numbers of fine, curving collections of fibres to join the roots of the vagus and spinal-accessory, remaining itself however a bundle of some size, even to its upper extremity, where it makes a curve and passes over in toto into the nervus glossopharyngeus. This curve is accomplished by the aid of a small mass of the small nerve-cells above referred to, that lie as it were in a trough formed by this the principal root of the glossopharyngeal nerve (Clarke).

2. The *median roots of the nervus vagus*, which, derived from certain fibræ rectæ of the raphe, run outwards between those roots of the hypoglossal nerve that also emerge from the raphe and the nucleus of the same nerve, and pass over, as the anterior limiting fibres of the ventricular gray substance, into the main root of the vagus (fig. 280, *X*, *X*). In all probability other members of the lateral system besides the vagus originate in this same manner.

3. The roots from the ganglia forming the *posterior column of origin of the lateral mixed system*, which has been described as comprising certain nuclei of the vagus and accessorius, as well as of the glossopharyngeus. The root-fibres passing off from their respective nuclei run to the inner side of the ascending common root above described (figs. 280, 281, X^1, XI^1).

4. Roots of the vagus which have their origin in the *fasciculus* (eminentia) *teres* (*Clarke*).

5. Fibres from the *gelatinous substance* (fig. 280, *G*) associated with the *ascending roots* of the 5th nerve, which attach themselves to the main roots of the vagus and glossopharyngeus, during their passage through the region occupied by these roots (*Clarke*).

6. Roots from the anterior column of origin of the lateral system, which I have been able to trace, on almost every section from the region in question, in unbroken continuity into the main roots of the vagus and glossopharyngeus (fig. 280, X^2). They form for both these nerves, inasmuch as they run parallel with the main root for a certain distance toward the ventricular gray substance and then, before reaching the same, turn back to join the main root, a sort of knee (genu) analogous to the knee of the facial nerve, from which it is however distinguished by the absence of the perpendicular connecting piece.

The lateral position of this last nucleus, which is typically the same with that of the inferior nucleus of the facial nerve, and the motor nucleus of the 5th nerve, as well as the form and size of its component cells, justify to the roots which spring from it the designation of *motor roots of the lateral system.*

7. The inferior roots of the nervus accessorius that spring, as far down as to the level corresponding to the lower end of the region occupied by the decussation of the anterior pyramids, from the processus lateralis of the anterior column of the spinal cord, and, to speak more exactly, not so much from nerve-cells that lie in the same plane with the main root of the nerve, as from more distant collections of cells from which the fibres pass in curves to their destined positions (*Stilling*, *Lenhossek*, *Clarke*, *Deiters*). Below the region occupied by the decussation of the pyramids, the cells of origin of the accessorius lie in the meshes of the reticulated structure to the outer side of the processus lateralis, into which the respective part of the anterior cornu is broken up (formatio reticularis), and the nerve-roots which, at the level at which they first began to make their appearance, directed their course forwards, and at the next lower level passed transversely through the lateral column (figs. 281 *XI*, 284, *XI*), now run in the immediate neighborhood of, and parallel to, the posterior cornu, although always without passing through its gelatinous substance. The last-mentioned limitation holds good for the collective roots of the accessorius (*Stilling*) (fig. 281 *XI*).

The *nuclei of origin* of the *nervus hypoglossus* lie by the side of the median line of the tubular gray substance, in the region of the open ventricle interiorly to, after the closure of the central canal anteriorly to, the common nuclei of the vagus and accessorius, and lie further enclosed in the roots of the hypoglossus themselves at their central extremity. In the nuclear mass on each side of the median line, an *inner* and an *outer* nucleus are to be distinguished, lying side by side (fig. 281 XII^1, XII^2), and both separated, by means of the fibres which they receive from the raphe, from a collection of small-sized nerve-cells that make up the anterior nucleus, which lies embedded among the fibres of the main roots of the nerve. The large outlying cells of the nuclei of the hypoglossus, that are to be found scattered for some distance among the fibres of the raphe, measure 60 μ in length by 21 μ in thickness, and lie with their long axes parallel to, and in the closest apposition with, the curves of the coiled fibres that are disposed within the two posterior nuclei in a manner immediately to be described.

I will preface this description, however, by speaking of the connection which exists between the nuclei of the hypoglossus and the posterior (reflex)

division of the oblongata, traversed as it is by fibræ arcuatæ, which, besides their other relations, take part in the formation of the posterior spinal columns. To the outer side of the hypoglossus roots, fine gray bundles of nerve fibres are to be seen passing directly forwards in radiating lines from the neighborhood of the nuclei of origin of the hypoglossus, in which

Fig. 281.

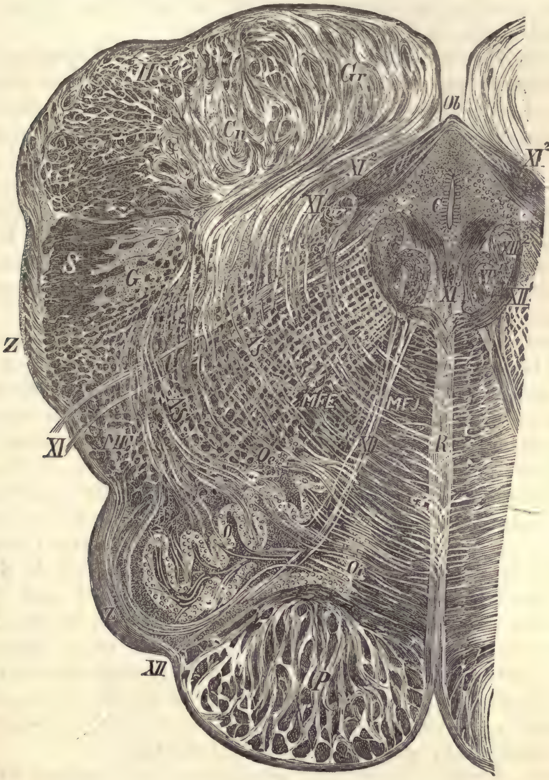

Fig. 281. *Transparent cross-section from the Human oblongata just below the level of the point of the calamus scriptorius.* *C*, central canal; *P*, anterior pyramid; *O*, inferior olivary body; *M E*, nucleus of the lateral column not far from its free outer surface and posteriorly to the olivary body; *S*, region of the tuberculum cinereum Rolando (ascending roots of the 5th nerve); *G*, gelatinous substance with transversely-cut fasciculi of the ascending root of the 5th nerve; *Z*, the stratum zonale, constituting posteriorly what remains of the inferior extremity of the corpus restiforme; *H*, posterior column of the oblongata with the nuclei of the funiculus cuneatus (*Ca*), and the funiculus gracilis (*Gr*); *Oe*, and *Oi*, external and internal accessory olivary bodies. *R*, the raphe; *MFJ*, *MFE*, inner and outer divisions of the motor district (anterior and lateral columns); XII^1 and XII^2, coils of the inner and outer nucleus nervi hypoglossi respectively; *XII*, main root of the hypoglossus; *XI*. main root of the accessorius. XI^1, nucleus nervi accessorii; XI^2, one of the nuclei accessorii in connection with the commissure contained in the obex (*Ob*); *W*, the ascending root of the lateral, mixed system; *AS*, fibræ arcuatæ.

without doubt they originate. They terminate in large cells which lie with their long axis parallel to the course of the fibres, about 0.25 mm. anteriorly

to the nuclei mentioned, and whose processes stand plainly in connection with the fibræ transversæ of the region. These radiating fibres are largely concerned, by reason of their decussation with the fibræ transversæ, in producing the appearance seen on cross-sections, of the division of the surface into minute districts which owe their origin to the anastomoses of the fibræ transversæ themselves (fig. 281, between *XI.* and *XII.*) This system of fibres, as well as those roots of the lateral system described under 6, p. 748, come under the general head of the radiating fibres (Radiärbündel) of the oblongata, as described by *Lenhossek.*

The long *fibræ rectæ* that unite the nuclei of the hypoglossus with the anterior pyramids apparently stand in connection with the *diffused nuclei pyramidales* of *Stilling*, cell-clusters which are especially well developed along the inner border of the pyramids, and whose elements resemble exactly those of the anterior division of the pons. These cell-clusters are at the same time in connection with certain fibres of the stratum zonale that terminate interwoven among the fasciculi of the pyramids, and it therefore appears probable that the hypoglossus, so far as it is in relation with the anterior tract of the crus cerebri, is brought, by means of the fibres of the *colliculus pontis* (Vorbrückchen), which still lies on the surface of the pyramids, into connection with the cerebellum.

These fibres derived from the crus cerebri pass over then finally, after being wound into a coil within the hypoglossal nuclei, into the *root of the hypoglossal nerve.* The central extremities of the coiled fibres are placed in connection with the fibres of the raphe, by means of the most posterior set of the *fibræ arcuatæ*, which are the prolongations of the long fibræ rectæ mentioned above. After passing along the outer border of the two nuclei of the nerve in question, and making their way gradually into the substance of the latter, where they enter into connection with their multipolar nerve-cells, these coiled fibres, originally fibræ arcuatæ, emerge from the same nuclei along their inner border, and join the main root of the nerve, which runs for the most part between the respective pyramid and olivary body, but to some degree through the substance of the olive, to the outer surface of the oblongata. The not infrequent occurrence of an apparent sudden termination of some of these fibres, during their passage through the olivary nucleus, led *Lenhossek* and *Schroeder v. d. Kolk* to the erroneous belief in the existence of a connection, by means of the so-called pedunculus olivæ, between the nervus hypoglossus and the olivary body.

All observers, lately also *Gerlach*, describe a *direct* passage of fibres from the crus cerebri into the hypoglossus by way of the raphe. These fibres, which become the innermost of those composing the roots of the nerve, make their way transversely among the most posterior fasciculi of the district occupied by the respective anterior column, describing curves which, contrary to those described by the fibræ arcuatæ, have their convexities directed backwards (fig. 281, *XII.*)

It is at the same time not to be proved, especially as regards their passage through the raphe, that these fibres are not interrupted in their course by nerve-cells, like the rest. Supposing them, however, to pass uninterrupted, we have no more than a repetition of one of the modes of origin of the facial nerve.

Gerlach has described a set of very fine commissural fibres, that pass between the hypoglossal nuclei of the two sides, through the gray substance that occupies the median line, posteriorly to the anterior columns, and *Clarke* has demonstrated on longitudinal sections a connection lying within the central tubular gray matter, between the common nucleus of the facialis

and abducens, and the nuclei of the hypoglossus. It is certain that many obscure anatomical details respecting connections of this kind are still to be discovered, which will throw much light on the underlying mechanism of the phenomena of co-ordinated reflex motions.

The fibræ arcuatæ of the posterior division of the oblongata constitute, above the region occupied by the decussation of the pyramids, seven sets, *counting from before backwards*, which stand in connection respectively with the following different parts: 1, with the corpus restiforme; 2, with the posterior columns (funiculi cuneatus et gracilis); 3, with the inner division of the pedunculus cerebelli; 4, with the roots of the auditory nerve; 5, with the ascending root of the mixed lateral system; 6, with the nuclei of the glossopharyngeus and of the vagus and accessorius; 7, with the nuclei of the hypoglossus.

5. The Cerebellum.

The cerebellum, that nervous centre situated posteriorly to the caudex cerebri, which played such a prominent part in the formation of that section

Fig. 282.

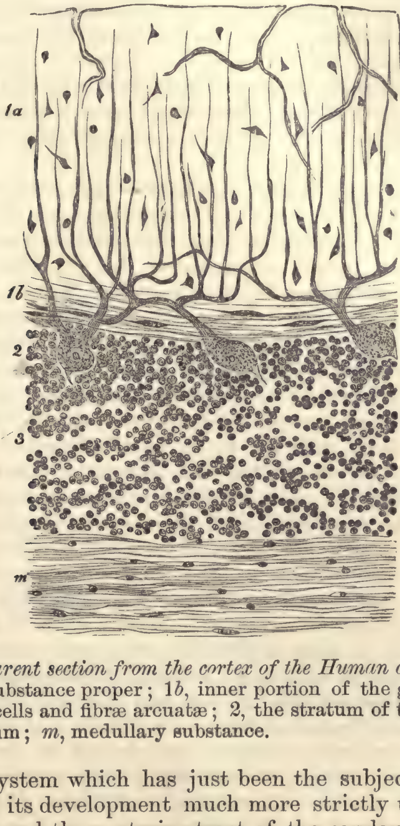

Fig. 282. *Transparent section from the cortex of the Human cerebellum.* 1*a*, outer portion of the gray substance proper; 1*b*, inner portion of the gray substance proper with spindle-shaped cells and fibræ arcuatæ; 2, the stratum of the cells of *Purkinje*; 3, the granular stratum; *m*, medullary substance.

of the projection-system which has just been the subject of our consideration, keeps pace in its development much more strictly than do the ganglia of the tegmentum and the posterior tract of the caudex, with the cerebral lobes. The preservation of this relationship holds good more especially for the lateral regions, the hemispheres, of the cerebellum, whereas the vermi-

form processes attain their greatest prominence in the lower brain types. Within these hemispheric portions again it is the anterior regions of their upper surface, the alæ of the central lobe and the two anterior or quadrate lobes, that find in the Human cerebellum their highest development (Huschke).

The gray substance of the cerebellum may be divided into three categories: 1, the *cortex cerebelli;* 2, the *nucleus dentatus*, situated in the medullary substance of the hemispheres; 3, the *nucleus tegmenti* of *Stilling*, situated in the medullary substance of the vermiform process.

1. The *cortex cerebelli. Obersteiner* has discovered that the *three* strata of the cortex cerebelli described by *Purkinje* are, in the cerebellum of the fœtus and the new-born Child, enclosed by a fourth external stratum made up of closely packed formative cells, which subsequently assume a spindle-shaped form, and become transformed into the connective-tissue fibres of the innermost lamina of the pia mater. This enveloping layer of connective tissue supports the thickened conical extremities of the trabecular fibres that project perpendicularly inwards, calling to mind the trabeculæ of the retina. They have met with special attention at the hands of *E. Schulze*, *Bergmann*, and *Deiters*, and *Obersteiner* found them to be in connection with the reticular stroma, and traced them, in the cortical substance of a cerebellum where the surrounding parts had been washed out, as it were, by a destructive encephalitic process, to the inner border of the stratum of purely gray substance.

The remaining strata are to be distinguished into, 1, that formed by the *gray substance proper ;* 2, the intermediate narrow stratum containing the *large cells of Purkinje ;* and 3, the innermost *grayish red* or *granular* stratum (fig. 282, 1*a*, 1*b*, 2, 3).

The *first stratum* is very rich in a reticulated, molecular basement substance, exactly resembling the connective basement substance of the cerebral lobes, and is regarded by *Stilling* as nothing but a felting made up of the finest possible ramifications of the processes of the ganglion-cells. Embedded therein lie, besides the apparently free nuclei of the connective tissue, also small (6–10 μ in length), three-cornered (pastile-shaped), and sometimes spindle-shaped nerve-cells. Their protoplasma is so destructible, that more difficulty is met with here than in the cortex cerebri, in determining the true character of the nervous elements of this class. At the inner border of this stratum, disposed around the sulci between each pair of convolution-lamellæ, the small nerve-cells are to be found elongated into spindles and lying parallel to, and in connection with, a layer of transverse, fine varicose nerve-fibres (fig. 282, 1*b*), that certainly appear to represent a system of fibræ propriæ of the cerebellum. It is however impossible to pronounce unconditionally upon their character, because, as will be explained below, it is precisely around the bottom of the sulci that the processes of the great cells in the neighborhood are found disposed transversely, and it may be that they constitute the fibres in question. Whatever be their nature, it is certain that they are in connection with the small cells above referred to.

The *middle stratum* of the cortex cerebelli is made up of the great nerve-cells of *Purkinje* disposed side by side and forming but a single row (fig. 282, 2). The colossal bodies of these cells (60–70 μ in length by 20–30 μ in thickness) appear generally inflated and devoid of processes on the side towards the granular stratum, whereas the great processes which are directed outwards are always visible. According to *Kölliker*, *Deiters*, *Koschewnikoff* and *Hadlich*, from the inner side of each cell springs one and only one process, which, according to the last three authorities, passes over without branching into a medullated nerve-fibre. *Stilling* however has observed a

number of such processes, and *Gerlach* has found them to be in connection with the granules already referred to. *Hadlich* on the other hand considers the fibrillæ, which stand in connection with these granules, to be the ultimate ramifications of the finely-striated processes of the great cells that occupy the gray substance proper, whose terminal branches had already been observed by *Obersteiner* to turn back upon themselves on arriving near the outer surface of the cortex, and to enter a network of fibres with which the granules in question are united. He adduces in favor of this belief the fact that at the summit of each convolution-lamella, where the cells of *Purkinje* occur in the greatest number, the granular stratum attains its greatest development, whereas in the neighborhood of the bottom of the sulci, where the number of the cells is small, the granular stratum is thinner than at any other point. According to *Obersteiner*, the cells of Purkinje unfold their many branches, which appear on section disposed like the antlers of a Deer, in one and the same perpendicular plane, each cell giving rise not to a cone of fibrillæ but to a system of ribs of a leaf, as it were, so that the foliated arrangement which characterizes the structure of the medulla cerebelli would find its expression also in the structure of the cortex. Finally it has been shown by *Obersteiner* and *Hadlich* that the divergence in a transverse plane of the primary processes of certain of the cells of Purkinje, in virtue of which they stretch themselves parallel to the surface of the cortex, as is strikingly apparent when they are compared with the processes of the other cells that shoot directly toward the surface of the cortex, is characteristic of a type of ramification which prevails only among those cells that occupy such portions of the cortex as immediately surround the sulci.

The large cells themselves seem to me to be enveloped in a somewhat loosely fitting capsule composed of a hyaline substance, which extends to beyond the point of emergence of the processes. *Obersteiner* regards this capsule as a network of connective-tissue fibres, in which the cell is loosely enclosed.

The innermost stratum of the cortex, recognized even by *Purkinje*, and subjected to a careful investigation by *Gerlach*, bears the closest resemblance to the granular strata of the olfactory lobe. Its elements generally present themselves, on account of the excessive delicacy and destructibility of their protoplasm, as insignificant naked bodies (6 μ in diameter), the nature of which has been interpreted in threefold manner. *Gerlach* and *Kölliker* believed them to be connective-tissue elements, although *Gerlach* at the same time described them as enclosed by the inner processes of the great nerve-cells. *Henle* and *Merkel* looked upon them as lymphoid elements. *Stilling* regarded them as very small, multipolar nerve-cells, united together into a reticulum. The protoplasm in which these bodies are really enveloped, and from which proceed a number of processes that remain for some time without ramifying, although often enough well marked under other circumstances (fig. 258, *e*), appear in the cerebellum of the new-born Infant (as Dr. Fries of Vernak has demonstrated to me) very distinctly defined and of a peculiar uniform clearness, which causes these elements to call strongly to mind those making up the inner granular layer of the retina.

The medullary substance of the cerebellum is, within the limits of the convolutions, rich in bodies resembling free nuclei, but which are probably in part outlying elements of the granular stratum. A considerable part of them are however to be looked upon as connective-tissue corpuscles, as certain pathological changes, the same with those referred to at p. 662, have enabled me to satisfy myself completely.

According to *Stilling*, the medullary fibres of the cerebellum become woven

together into a network, a mode of disposition which is incompatible with the requirements of isolated conduction. The existence of such a structure has not been confirmed by any other observer, and one cannot help concluding that he mistook a reticulum of connective tissue for nerve-fibres, a mistake that might easily be made in dealing with preparations such as he employed, which have not been made transparent, and where the lines are obscured by the altered medullary sheaths. Indeed *Stilling* himself brings a powerful argument to bear against the existence of such a universal connection between the nerve-fibres, by calling attention to the fact that the hardened medulla cerebelli admits of being so easily split up into simple lamellæ.

2. The *nuclei dentati* discovered by Vieussens, lying near the lower, medullated surface of the cerebellum, which roofs over the 4th ventricle, consists of lamellæ of gray substance 0.3 mm. in thickness, which in Man are thrown into intricate folds, and each of them is provided, on its lower and inner surface, with a hilus through which its nerve-fibres find admission. By reason of being in the Human cerebellum so finely plaited, these nuclear masses bear a very striking resemblance to the inferior olivary bodies, and the nerve-cells of the two (30 μ in length by 12 μ in thickness) resemble each other exactly. Further, certain *nuclei dentati accessorii* are to be detected lying somewhat inferiorly and anteriorly to the main nuclei, to which they are inferior in size. The lamellæ of gray substance of which they consist are thicker than those first described (0.6 mm.), and they are made up of larger elements (45 μ in length by 15 μ in thickness). The folds of the latter nuclei are less fine and less closely disposed than those of the former, and the continuity of their outlines is repeatedly broken by the passage of large bundles of nerve-fibres. The nucleus *dentatus* of the lower Mammals (even of the Ape, fig. 278, *D D*) does not present the same distinctness of outline or the same delicate foldings with that of Man, but appears inflated, by an excessive quantity of connective tissue, to a simply curved mass of gray substance.

3. The *nuclei tegmenti* of *Stilling* are two rounded masses which, in the Human cerebellum, lie beneath the central lobe of the superior vermiform process. Seen from above, they have a rhomboidal shape. They measure 5 mm. in length and breadth by 2 mm. in thickness, and by careful manipulation may be separated from their surrounding connections. They are divided off from one another by a narrow lamina of medullary substance that occupies the median line, and are traversed by medullary fibres in great numbers. The large elongated nerve-cells of which they are made up (60 μ in length by 15 μ or more in breadth) exactly resemble those of the outer auditory nucleus (fig. 278, *T*).

What we know of the *course of the nerve-fibres* in the cerebellum is but fragmentary and general. *Stilling's* work, in which the subject is treated on a very large scale and attention paid to the minutest anatomical details, has not proceeded as yet beyond the consideration of the lingula and the lobus centralis. It is established beyond a question, however, that there exist, within the medullary substance of the organ in question, systems of *fibræ propriæ*, *i. e.*, fibres which have their origin and termination within the cerebellum itself, besides the systems of fibres which belong to the processus, which pass to different regions of the caudex.

1. *Fibræ propriæ*. *Burdach*, *Arnold*, and *Stilling* (the latter in consequence of the study of cross-preparations) have all taken cognizance of the fibræ propriæ *in general*, *i. e.*, bundles of fibres passing festoon-like from convolution to convolution along the surface of the cortex, disposed in

delicate laminæ. *Stilling* describes further certain more comprehensive *special* systems of *fibræ propriæ* which unite together more distant regions of the cortex cerebelli. He designates them as median fasciculi. An anterior division of them runs, split into two parts, from the anterior regions of the superior vermiform process by the shortest path beneath the *nucleus tegmenti* directly to the lobuli of the inferior vermiform process, *i. e.*, from the *lingula* to the *nodulus.* Another division of these median fasciculi, whose course is concentric with, but embraces that of the first division, also divided into two parallel parts, runs at first backwards in a curve whose convexity is directed upwards towards the superior vermiform process, then bends forward again to terminate in the most anterior of the convolutions of the inferior vermiform process, thus bringing the latter for the second time into connection with the most anterior convolutions of the superior vermiform process, though by a very circuitous route. Besides these systems of fibres, the cerebellum encloses also a considerable mass of *transverse commissural fibres*, which probably, like the trabecular system of the cerebrum, unite together exactly symmetrical regions of the two hemispheres.

2. The *processus cerebelli.* Of these tracts, as far as they lie within the limits of the cerebellum, the processus ad pontem and certainly a large part of the corpus restiforme (outer division of the processus ad oblongatam) follow a very simple course. Their component fibres decussate, as described above, before reaching the cerebellum itself. Having entered the cerebellum, they remain, up to the moment of their entrance into the cortical substance, confined each to its own side, although, to be sure, in so far as they enter into connection with the median regions of the cortex, a part of their fibres run inwards as if about to decussate.

The relative position occupied by the processus within the cerebellum itself, is determined by the situation of the masses of gray substance in which they respectively terminate. The *processus ad pontem* and the *corpus restiforme* enter into connection solely with the cortex, while the *processus ad cerebrum* becomes connected primarily with the *nucleus dentatus*, and the inner division of the *processus ad oblongatam* with the *nucleus tegmenti.* Since now the cortex occupies the most external position of all the gray masses, while the nucleus dentatus lies more centrally, between the cortex and the nucleus tegmenti, which is the innermost of all, it is evident that the medullary substance of the cerebellum must be divided up among the different processus, in such a manner that its outermost regions are occupied by the *processus ad pontem* and the *corpus restiforme*, its central regions by the *processus ad cerebrum*, its innermost regions by the above-mentioned *inner division of the pedunculus* (fig. 278, *Br*, *St*, *B*, *H.*[1])

The nucleus dentatus is further immediately covered over by a smooth separable layer of fibres belonging to the corpus restiforme, that bury themselves in the irregularities of its surface and perhaps even enter into connection with its nerve-cells.

The *processus ad cerebrum*, that underwent their decussation within the limits of the tegmentum cruris cerebri, pass, like the other processus, directly into the substance of the cerebellum, and make their way each to the hilus of its respective nucleus dentatus (Gratiolet), arrived within which, its fibres diverge like radii toward the nerve-cells that stretch out to meet them. These tracts do not, however, remain through their whole course through the cerebellum to the hilus of the nucleus dentatus, free from admixture with other systems of fibres, but, on the contrary, just as they are traversed during the free part of their course by fibres belonging to the 5th nerve, so here they are traversed in every direction by fibres belonging to

the various systems of the neighborhood, and especially by those belonging to the *inner division* of the *pedunculus cerebelli.* The fibres composing this last-mentioned tract follow, to all appearance, a twofold course. Of the innermost of them, one part pass directly into the nucleus tegmenti ventriculi of the same side, while another part, curving along the upper border of this nucleus, make their way without question into the corresponding nucleus of the opposite side (fig. 278, H^1). On their way they penetrate a narrow layer of nerve-fibres occupying the median line, a sort of raphe, that lies between the opposing nuclei tegmenti, and, inasmuch as the fibres of which it is composed run from before backwards (*Stilling's* median fasciculi), presents on section-preparations a very opaque appearance. Within this raphe the opposing sets of fibres decussate, and each of them then makes its way into the tegmental nucleus of the opposite side near its lower border. Supposing them to pursue their course further in the same direction, it is manifest that these fibres penetrate next the medullary substance of the inferior vermiform process, where they are probably brought into connection with the cortical substance of the inferior portion of the hemispheres, through the agency of the commissures enclosed in this medullary substance, which find their way into all the regions of this section of the cortex. The most anterior of these commissures is the *velum medullare posterius*, that is united by a fasciculus of the pedunculus flocculi with the cortex of the flocculus.

A second fasciculus of the pedunculus flocculi passes, as is well known, over the auditory nerve to the lateral wall of the ventricle, within which it takes an upward course, returning probably at a higher point, in company with the pedunculus cerebelli, into the cerebellum. (Fig. 278, *F.*)

The *outer* bundles of fibres of the inner division of the pedunculus cerebelli (fig. 278, H^2) pass, after making their way through the processus ad cerebrum, without undergoing decussation, directly into the cerebellar medullary substance, leaving the nucleus tegmenti to their inner side.

In short, the component fibres of this *inner division* of the *pedunculus cerebelli* traverse the substance of the cerebellum in so many different directions, that they may well be supposed to enter into connection with all sections of its cortex, as well as with the processus ad pontem and the corpus restiforme.

The course taken by the system of fibres by which the auditory nerve is represented in the cerebellum remains, as regards the question of their subsequent decussation, as yet uncertain. Those fibres of the *anterior main root* of this nerve that, within the limits of the posterior division of the pons Varolii, do not cross the median line (fig. 278, 8^4, and the corresponding fibres of the opposite side), certainly do not decussate subsequently in the cerebellum, but make their way directly through the processus ad cerebrum and the nucleus dentatus of the same side. Whether those fibres of the *anterior* and *posterior* main roots, however, which do cross the median line within the region of the pons, remain permanently in that hemisphere of the cerebellum into which they first make their way, and where they are not to be distinguished from the component fibres of the inner division of the pedunculus cerebelli, is still uncertain. In fact it is impossible to say with certainty whether the collective fasciculi of this inner division of the pedunculus do, or do not, constitute really a part of the auditory tract. However that may be, certainly those of these fasciculi which decussate as described between the nuclei tegmenti ventriculi, must necessarily, in so doing, cross the median line for the second time, as we have seen that all the component fibres of the inner division of the pedunculus pass over

below, *i. e.*, within the posterior division of the pons, into fibræ arcuatæ (p. 745).

The opinion already expressed by *Kölliker* and *Deiters*, that the cerebellum serves to establish, by virtue of the peculiar and varied arrangement of its component fibres, that in general are disposed in the form of loops, an indirect communication between the nerve-roots and the cerebrum, finds no stronger support than in the fact that the auditory nerve, which stands functionally in such intimate relation to the cerebrum, probably buries itself entirely, so far as its immediate connections are concerned, in the substance of the cerebellum.

The well-known relation of the cerebellum to muscular sense presupposes the passage of other nerve-tracts, besides that of the auditorius, through that nervous centre, on their way to the cerebrum. That the cerebellum, however, cannot represent anything more than an important way-station for the impressions derived through the nerves of muscular sense, is shown by the fact that they, like sensory impressions of every kind, are taken cognizance of by consciousness, which thereby, to use Wundt's happy expression, gives the signal of their arrival within the cerebral lobes. Any attempt to bring out of the chaotic mass of possibilities that is presented to us, a definite statement of the connections existing between the various systems of nerve-fibres that come together there, must necessarily, with our present knowledge, be limited to supplying suggestions rather than facts, and would therefore be out of place in a treatise which pretends to regard the subject from a morphological point of view. From a morphological point of view, then, two facts only are of interest in this connection, both of which tend to support the theory that the different systems of nerves are diverted within the cerebellum from their original course. The first of these facts is that observed by *Obersteiner* and *Hadlich*, that the secondary processes of the great nerve-cells of *Purkinje* are really so bent that the direction of their original course is essentially changed; the second has to do with the unique form of these nerve-cells themselves.

The cells of Purkinje are in fact, in a morphological sense, bipolar. Their inner and outer ends may be regarded as the rudimentary representatives of two different types of nerve-cells. In other words, if it were possible to divide these great cells, "flask-shaped," as they are generally called, into halves, and to unite together the similar halves of different cells, the newly constructed elements would differ fundamentally in their character. Those formed from the inflated halves, the bodies of the flasks, that are turned toward the granular stratum, each furnished (probably) with its single slender process, would resemble those globular cell-forms, almost devoid of processes, that are found in the spinal ganglia, in the *Gasserian* ganglion, and in the descending roots of the 5th nerve (*v.* p. 705), in connection with *sensory* nerve-roots. Those, on the other hand, formed from the union of the outer halves, the necks, of the flask-shaped cells, that taper off gradually into the massive processes which are directed toward the outermost stratum of the cortex, would resemble the elongated cell-forms, furnished with a number of large processes, that make up the nuclei of origin of the *motor* nerve-roots.

Each of the cells of *Purkinje* therefore (if it be taken for granted that their inner processes do really, as *Deiters*, *Koschewnikoff*, *Hadlich* have affirmed, pass over without branching each into the axis cylinder of a nerve) may be supposed to be in connection, through that extremity which has the form characteristic of the sensory cell, with a *centripetal nerve-fibre*, and through that extremity which has the form characteristic of the motor cell,

and from which the branching processes proceed, with *several centrifugal nerve-fibres.* We have seen moreover that of the two processus cerebelli, the corpus restiforme and the processus ad pontem, the former, which contains the fewer nerve-fibres of the two, is the continuation of the posterior column of the spinal cord, while the latter, by far the richer of the two in nerve-fibres, is in connection with the basis cruris cerebri, a motor nerve-tract, *i. e.*, so far as it is derived from the nucleus lenticularis and nucleus caudatus. In fact the ratio of these two tracts to one another, in point of size, seems about equal to the ratio of the *two varieties of the nerve-cell processes* to one another *in point of number*, whereby an additional reason is furnished for regarding each of the large cells in question as a node, an articulating joint as it were, serving to effect the transition of a nerve of a certain kind into a number of other nerves, whose functional significance is the opposite of its own.

6. The Transition from the Structural Type of the Oblongata to that of the Spinal Cord.

We have seen that in the region of the oblongata, inasmuch as it was divisible into an anterior and a posterior tract, the same duplex organization prevailed as throughout the entire caudex cerebri, where it first found expression in the general division of the cerebral ganglia into two groups, and more strikingly in the division of the crus cerebri into *basis* and *tegmentum.* We have seen further that the *organization of the crus cerebri* was modified by the arrival of a certain system of nerve-fibres, the *pedunculus cerebelli*, which took part in the organization of the medulla oblongata by furnishing, on the one hand, the greater part of the fibræ arcuatæ of that region, and on the other hand, certain masses of ganglionic matter which stand in connection with its fibres, and which occur partly in the compact form of the olivary bodies, and partly in the form of the systems of scattered cells.

The organization of the spinal cord, the formation of which we are about to trace, differs from that of the oblongata in four respects, which are as follows: While the oblongata is made up (1) of the continuation of the *anterior* and *posterior* tracts of the crus cerebri, to which (2) a *third* tract, the pedunculus cerebelli, is subsequently added, the columns of the spinal cord, which are formed from these three fibrous tracts, constitute a symmetrical, essentially *homogeneous* and continuous investing sheath of *nerve-fibres*, which does not present the least trace of the *three tracts* that characterize the organization of the oblongata, nor of the two tracts of the crus cerebri. Further, while (3) in the region of the upper half of the oblongata the central tubular gray matter is spread out to form the floor of the 4th ventricle, within which the nuclei of origin of the sensory and motor nerve-roots lie side by side, or *inwardly* and *outwardly* with respect to the median furrow of the ventricle, in the spinal cord, on the contrary, this same gray matter is so disposed as to enclose a narrow opening, the central canal, and the sensory and motor nuclei are arranged one behind the other, or in other words anteriorly and posteriorly to this central opening. Finally (4), in the place of the many and varied masses of gray matter of the oblongata, the central tubular gray matter of the spinal cord, disposed as just described, forms the only and single ganglionic mass.

These morphological differences are removed essentially through two important processes, viz., through the process which effects the formation of the posterior columns and the consequent *enclosure of the central canal*

which takes place within the limits of the upper half of the oblongata, and through the *decussation of the anterior pyramids* which occurs within its lower half.

1. *The enclosure of the central canal.* Below the transverse line drawn through the widest part of the 4th ventricle (*v.* fig. 280) the fasciculi of the corpus restiforme, *i. e.*, the outer division of the pedunculus cerebelli (*M F C*), resolve themselves gradually, as we have seen (p. 724, seq.), into fibræ arcuatæ which make their way through the olivary bodies and finally gather themselves together, at the inner side of the opposite corpus restiforme, into the funiculi gracilis et cuneatus (the posterior column of the oblongata, *i. e.*, the future posterior spinal column), and it is evident that, in consequence of this process, each restiform body must decrease in size, and each posterior column, which lies to the inner side of the corresponding restiform body, increase in size, at exactly the same rate. It is further evident that if successive portions be constantly taken away from one end of a given area, and other portions correspondingly added to it at the other end, the area will move in the direction of the additions. In similar fashion the pedunculus cerebri, by reason of the constant additions made to its *inner* division, the posterior column, and the constant deduction from its *outer* division, the restiform body, gradually moves inward toward the median line. In so doing it necessarily drives inwards before it the external column of nuclei, the sensory portion of the gray substance that forms the floor of the 4th ventricle, which impinges on the newly formed posterior column, and which gives origin to the roots, at first of the auditory, lower down of the vagus nerve. In the course of this process the 4th ventricle becomes of course deeper and deeper, and the above-mentioned column of nuclei, which lay originally *to the outer side of the nucleus of the hypoglossal nerve*, lies finally *behind* that same nucleus (comp. figs. 280 and 281). Finally, crowded more and more inwards, these columns of nuclei of opposite sides, now the *posterior nuclear columns* of the central gray substance, and after them the opposing *posterior fibrous columns*, which have been constantly increasing in size and thereby approaching the median line, are respectively brought so near each other that their inner surfaces come into contact. The apposed surfaces of the two columns of gray matter then become fused together, whereby the *enclosure of the central canal is finally made complete.* Between the two fibrous columns, however, remains an interval, the posterior fissure of the oblongata. By this process one step has been made toward the structure of the spinal cord (fig. 281 *C*). The importance of this step will moreover appear much more considerable if it be taken into consideration that in its essential features, *i. e.*, apart from the relative position of its special masses, the conformation characteristic of the gray substance of the cord is to be traced in the gray substance of the oblongata. The nuclei of the hypoglossus that lie near the median line, far removed from the pedunculi cerebelli, remain unaffected by the change in the position of the latter, and pass over, without changing their own position, into the inner portions of the anterior cornua of the cord. Below the level corresponding to the lower extremity of the inner accessory olivary bodies these nuclear masses give rise, no longer to hypoglossus roots, but to the roots of the anterior cervical nerves, beginning with the first (*Stilling*). The processus lateralis of the anterior cornu has likewise its representative in the region of the oblongata, viz., in the anterior column of origin of the above described mixed, lateral system of nerve-roots. On account of the constantly decreasing size of the oblongata, however, this column of nuclei soon becomes unable to retain an independent position so

far removed from the anterior cornu, and finally, at the level of the lowest roots of the accessorius, it becomes completely fused with the latter formation.

The posterior cornu, on the other hand, is represented, even in the oblongata, by a coherent mass of gray substance. As it appears in the spinal cord it is made up of the *caput*, the *cervix*, formed essentially of the posterior nerve-roots in their passage outwards, and the *triangular-shaped basis* which is fused with the rest of the central tubular gray matter, and to which *Goll* has given the appropriate designation of the *trigonum cervicale cornu posterioris.* The *nucleus of the vagus nerve*, which forms the anterior outer projection of the central gray substance of the oblongata, corresponds exactly to this triangular mass. The *caput cornu posterioris* is represented in the oblongata by the gelatinous substance which is associated with the ascending roots of the fifth nerve. Finally, this gelatinous substance is traversed, as has been mentioned, by the fibres of the main root of the vagus, which at their central extremity enter the point of the *trigonum cervicale, i. e.*, the nucleus of the vagus, and which represent, therefore, the *cervix cornu posterioris.* The posterior cornu of the oblongata, however, although morphologically exactly similar to that of the spinal cord, instead of being directed *outwards and backwards*, is directed *outwards and forwards.* The change in its position takes place as follows:—

It has already been mentioned that the nucleus of the vagus nerve (outer nuclear column of the gray substance) makes a partial revolution inwards toward the median line. The main roots of the vagus that are in connection with this nucleus also take part in this partial revolution, and since the gelatinous substance through which these roots pass moves backwards in company with them, the entire posterior cornu is thus brought gradually into the transverse position which it occupies in the lower half of the oblongata, as is shown by the direction of the course taken by the nerve-roots, no longer those of the vagus, but the posterior roots of the cervical nerves. (Fig. 284, left-hand side.) It is now only the great thickness of the posterior fibrous columns interposed between the two posterior cornua that prevents the latter, disposed as they are, like radii in the cylindrical oblongata, from continuing their revolution toward the posterior fissure, a third radius, as it were, or in other words from assuming the position which they are to occupy finally in the spinal cord. The great width of the posterior columns at this level is due, however, not to the great number of their component fasciculi, but to the presence of certain masses of gray substance, the nuclei of the fasciculi gracilis et cuneatus, and the final change in the position of the posterior cornua is brought about by the disappearance from the posterior columns of these nuclear masses, that remain embedded in them only until the formation of the posterior columns is rendered finally complete by the accession of certain fasciculi from the anterior pyramids. (Figs. 281, 283, 284.)

At the same time with the removal of the difference that existed between the structure of the oblongata and that of the spinal cord in respect to the conformation of the tubular gray matter, that difference, also, that was due to the part taken in the organization of the oblongata by the *pedunculus cerebelli* is removed by the passage of the *corpus restiforme into the posterior columns.* In other words, with the completion of this process, the systems of *fibræ arcuatæ* by which it was effected *disappear*, and with them the collections of gray matter with which they were in connection, *i. e.*, the *olivary nuclei of the oblongata*, and the *systems of scattered nerve-cells.* Further, since the enclosure of the central canal is directly dependent upon

the formation of the posterior columns, these two changes cannot be studied as separate processes.

At that level at which the enclosure of the central canal is complete, the conformation of the oblongata is such that the following regions may be traced upon its outer surface. (Fig. 283.)

1. On each side of the median line lie the anterior pyramids (*P*), the continuation of the basis cruris cerebri as yet undiminished in size. 2. Next comes the outer surface of the region occupied by the posterior division of the caudex cerebri; the continuation of the tegmentum cruris, which is destined to pass over directly into the antero-lateral column of the cord (*Oi*—*G*). The rest of the respective half of the oblongata, posteriorly to this region, is occupied by the posterior column, on the surface of which the following three formations may be traced. Bordering on the antero-lateral column lies (3) the gray mass of the tuberculum cinereum *Rolando*, dimly visible through the sheath of nerve-fibres that surround it. It represents again the caput cornu posterioris, which, however, is in no other

Fig. 283.

Fig. 283. *Transparent cross-section from the inferior half of the Human oblongata, in the region of the superior decussation of the pyramids.* *C*, the central canal; *P*, the inner and middle fasciculi of the pyramids; *P*', the outermost fasciculi of the pyramids; *G*, gelatinous substance of the tuberculum cinereum Rolando; *H*, posterior column; *Cn*, nucleus funiculi cuneati; *Gr*, nucleus funiculi gracilis; *Oi*, oliva accessoria interna; *XII*, roots of the nervus hypoglossus; *D*, place of decussation of the external fasciculi of the anterior pyramids, that at *H* pass to the outer side of the gray substance surrounding the central canal, losing themselves finally in the funiculi graciles et cuneati; *A A*, fibræ arcuatæ in connection with the posterior column, but not with the anterior pyramids; *V*, the (future) anterior column.

region so enormously developed as here. Cross-section preparations show, within and around this gray mass, transversely-cut fasciculi belonging to the ascending root of the fifth nerve, that have their origin at a still lower level. Behind the tuberculum of Rolando (4) is to be seen, on cross-

sections, the *triangular* nucleus of the *funiculus cuneatus*, and (5) more interiorly, along the posterior fissure, the *club-shaped nucleus* of the *funiculus gracilis*, both embedded in the posterior column. (Fig. 281.)

2. *The Decussation of the Pyramids.*—Up to this point, the presence of the anterior pyramids as independent tracts has continued to give to the organization of the medulla a twofold character, which is removed through the following two processes :—

Through the first process, certain of the outermost fasciculi of the anterior pyramids become associated with the posterior columns, and the final organization of the latter becomes thereby completed. These fasciculi appear on cross-sections as delicate, clearly defined lines (fig. 283 P^1), passing inwards behind the middle and inner fasciculi of their respective pyramid to the raphe (D), where they decussate with the corresponding fasciculi of the other side. They then pass in curves to the other side of, and very near to, the gray substance surrounding the central canal, forming thereby the most inferior and posterior set of the fibræ arcuatæ, and lose themselves finally in the posterior column of the spinal cord. This is the *superior sensory decussation*, and the fibres that take part in it run in *delicate fasciculi. Clarke*, *Luys*, and *Deiters* have recognized the fact that the posterior columns receive fibres that have decussated with the anterior pyramids.

The question as to the plan of origin of these external fasciculi, which form the prolongation of the outermost fasciculi of the basis cruris cerebri, was discussed, p. 679. *Deiters* supports the opinion there expressed, by affirming that the component fasciculi of the basis cruris cerebri are prolonged into the anterior pyramids without undergoing any change in their relative position, and that the outermost fasciculi of the pyramids must be regarded, therefore, as identical with the outermost fasciculi of the basis cruris cerebri.

These outermost fasciculi of the pyramids probably do not, after their decussation, become associated exclusively with posterior spinal columns, but undoubtedly enter also into connection with such of the posterior roots of the first pair of cervical nerves as have their origin in that region, for these nerves would otherwise not be represented, as are all the others, by fibres from the anterior pyramids that have decussated at the median line.

On cross-sections from the region which is the seat of the above-described process, the fibræ arcuatæ which connect the pyramids with the posterior columns are enclosed (fig. 283, A A) by such as still remain of that other system of fibræ arcuatæ that pass from the pedunculi cerebelli to the posterior columns, as explained above. The former are to be distinguished from the latter by their posterior position, by their relation to the well-marked region occupied by the decussation (D) described above, by the greater diameter of the bundles into which they are collected, and by the fact that no gray ganglionic substance is inserted in their course from the pyramids to the posterior division of the oblongata. The fact that these two systems of fibræ arcuatæ exist side by side with each other, shows that only an ideal line can be drawn between that region of the oblongata which is traversed by the emissaries of the pedunculus cerebelli, and that which is the seat of the transition processes which we are now considering.

The process through which the twofold organization of the caudex cerebri is finally and completely reduced to the simple organization of the cord, consists in the *inferior decussation*, *i. e.*, the decussation of the *motor fibres of the pyramids*, gathered into *coarse fasciculi*, which takes place in the region immediately below that occupied by the superior decussation, *i. e.*, in the region of origin of the first and second cervical nerves.

In the course of this process, by far the greater part of the fibres of each

anterior pyramid pass, collected, as before mentioned, into thick fasciculi, across the median line (fig. 284, *D*), and lose themselves in the lateral column of the opposite side. This passage of the pyramids into the lateral columns takes place, as *Clarke* and *Lenhossek* have described it, without the intervention of ganglionic substance.

The fasciculi of the lateral columns, that at their emergence from the place of their decussation are disposed transversely, weave themselves among the fasciculi of those columns which were already lying in a longitudinal direction, dividing them into very small groups, which appear on cross-section as small, defined districts, thus giving rise to the *formatio reticularis*, which ceases to exist only in the upper part of the cervical portion of the cord (*Stilling*, *Clarke*, *Deiters*).

Fig. 284.

Fig. 284. *Transparent cross-section from the Human oblongata in the region of the inferior decussation of the pyramids.* *C*, the central canal; *P*, one of the anterior pyramids in process of resolution; *V*, the (future) anterior column; *L*, the lateral column; *D*, the decussating pyramids; *Cn*, cornu anterius of the gray substance; *G*, the caput cornu posterioris (tuberculum cinereum) still in apposition, posteriorly, with the remains of the nucleus funiculi cuneati; *H*, the posterior column; *XI* (white) one of the most inferior of the fasciculi belonging to the root of the nervus accessorius; *XI* (black), on the left-hand side within the anterior cornu), transversely-cut fasciculi belonging to the nervus accessorius, destined at a lower point to change the direction of their course and pass out as part of the main root of the nerve.

This formatio reticularis, to be sure, encloses, in its lower regions, great numbers of large nerve-cells in its meshes, but they are, as *Stilling*, *Lenhossek*, and *Clarke* have affirmed, only the cells of origin of the spinal-accessory nerve. A number of nerve-cells sufficiently great to serve as the terminal cells of so considerable a mass of fibres as take part in the inferior decussation of the pyramids is certainly not to be found, as *Deiters* affirmed, in the formatio reticularis, at least not in Man. It must be confessed that the corresponding collection of gray matter in the inferior Mammals, to which

Deiters refers as affording more conclusive evidence of the validity of his view, presents, far more than does the gray substance of the formatio reticularis of Man, the appearance of being present in sufficient quantity to interrupt the course of the collective fibres of the pyramids. But, on the other hand, the very fact that in the oblongata of these animals this collection of gray substance is so abundant, while the pyramids are relatively so poorly developed, indicates that the two formations exist independent of each other. In truth, however, the great size of this mass of ganglionic substance in the oblongata of the Calf and the Cat, which seems to afford support to *Deiters*' view, is due, not to an increase in the number of the ganglion cells, but to an excessive development of connective substance, such as characterizes in general the brain of the lower Mammals, in contra-distinction to that of Man.

It is evident, then, that the fineness of the component fibres of the pyramids, as compared with those which make up the lateral columns of the cord, to account for which *Deiters* felt obliged to assume that the course of the first-mentioned fibres was interrupted by nerve-cells, must be the result of some change taking place within the continuity of the fibres themselves.

Clarke and *Lenhossek* confirm the opinion expressed by Burdach, viz., that a certain portion of the fibres of the anterior pyramids do not take part in the decussation and in the formation of the lateral columns, but pass over, without crossing the median line, into a certain group of fibres belonging to the anterior columns of the cord (Burdach's fundamental fasciculi (Grundbündel) of the pyramids). *Stilling* and *Deiters* have not been able to confirm the truth of this statement.

Just as the posterior roots of the spinal nerves, which have their origin at the level of the decussation of the sensory portion of the anterior pyramids, are joined in all probability, as was shown above, by fibres that have taken part in the decussation, so also are the roots of the anterior nerves, according to Clarke's description, joined by fibres that decussate with the anterior pyramids and penetrate the anterior cornu of the gray substance.

With the passage of the last of the fasciculi of the anterior pyramids into their respective lateral columns, the nerve-fibres of the projection system, as well as its collections of gray matter, have become arranged in accordance with the structural type of the spinal cord.

Inasmuch as the component fibres of the lateral columns are not implicated in the decussation which takes place in the anterior commissure of the spinal cord, it is plain that they cross the median line but once, between the anterior pyramids, of which they originally formed a part, and the anterior roots of the spinal nerves in which they terminate; and they are, therefore, manifestly well fitted to conduct the impulses of the will from the cerebral hemisphere of one side to the muscular system of the other.

It is my pleasant duty to acknowledge gratefully, before concluding, the intelligent and artistic assistance afforded me by Dr. Carl Heitzmann and the artist Adolf Göhre, of Vienna, who executed for me the accompanying wood-cuts, the former, Figs. 253–260, further, 262, 263, 266–269, 282; the latter, the still greater number that remain unmentioned.

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BRAIN IN GENERAL, OR ENCEPHALON.

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CHAPTER XXXIII.

THE SYMPATHETIC NERVOUS SYSTEM.

By DR. SIGMUND MAYER.

THE so-called sympathetic or vegetative nervous system appears widely distributed in the animal body, more especially in those organs which are endowed with the functions of generative and vegetative life. The uniform and regular branching which is observed in the cerebro-spinal nervous system is much less marked in the sympathetic system; only the lateral cords of the sympathetic with the ganglia embedded in it in a regular series form a symmetrical type. Beyond this the cells and fibres of the sympathetic are distributed throughout the body in an irregular manner, and, as a rule, to the vegetative and generative organs. Whereas the cells of the cerebro-spinal masses may, through the cerebral and spinal nerves, influence organs provided with striated muscular fibres as well as those having smooth muscles, the nerve cells of the sympathetic have as yet been found (in Mammals) distributed to striped muscular fibres only in the heart.

At an earlier day there was great debate as to whether the sympathetic was to be looked upon as an independent nervous system, or as a dependence of the cerebro-spinal system. It has however been recognized that such a discussion is aimless. A look at the unmistakable communicating fibres which are met with between the sympathetic and cerebro-spinal systems can leave no doubt in the observer's mind as to the existence of the closest relation between the two sets of nervous organs The two systems may properly be regarded as functionally conjoined organizations; only that in the cerebro-spinal system the nerve cells form large masses, and that the union between its different parts is effected by means of fibres which do not leave the territory of the central organ, and which preserve the characters of central fibres, while, on the contrary, the nerve cells in the sympathetic are more widely separated one from another, and the union between these cells and between them and the cells of the cerebro-spinal axis takes place by means of peripheral nerve fibres. While the principle of centralization of elements is represented in the cerebro-spinal axis, that of decentralization is more pronounced in the sympathetic system.

The sympathetic is made up, just as is the brain and spinal cord, of cells and fibres; and here also the nerve fibres have their origin in nerve cells.

Inasmuch as they present certain peculiarities, it will be necessary to study more closely the two elementary constituents of the sympathetic; although we shall recognize in them the general character of nervous elements as laid down in the third chapter of this work.

The ganglion cells of the sympathetic are in part joined together in large groups, the so-called ganglia; in part scattered along the course of nerve trunks; or they lie disseminated in organs. The ganglia of the sympathetic possess an envelope of connective tissue which sends prolongations between the individual cells, and thus constitutes capsules for the cells. The

connective tissue therefore forms a compartment structure in which the nerve cells are embedded, and which at the same time supports the blood-vessels. Each ganglion has an afferent and an efferent nerve, the fibres of which take different directions in the ganglion; a part running from the periphery to the cerebro-spinal centre, another part in an inverse direction. As yet there is no character known by which one set of fibres may be distinguished from the other. The nerve cells lie in the midst of a maze of fibres, so that an insight into the mode of union between nerve fibres and nerve cells can be obtained only by a minute study. Nerve cells are also found scattered along the course of small nerve trunks, and they here lie either in them or on their sheaths.

The nerve cells of the sympathetic exhibit essentially the characters of nerve cells as they have already been described in the third chapter of this manual; and they possess but few peculiarities by which they can be distinguished from the central cells of the cerebro-spinal axis. Just as in various localities in the brain and spinal cord, nerve cells exhibit variations as regards shape, size, number of processes, configuration and number of nuclei, etc., so throughout the sympathetic system nerve cells do not everywhere present the same aspect.

Shape. The shapes most commonly assumed by sympathetic nerve cells are the oval, round, pear, or spindle-shaped. Bidder has described cells from the cœliac ganglion which exhibited rectilinear outlines and which were arranged in rows like blocks. I have often seen a similar formation in the sympathetic of the Frog.

Size. In one group of ganglion cells forming part of one ganglion there may be observed the greatest differences in size; so great indeed, that a cell may lie next to one which is four times its own size.

Fig. 285.

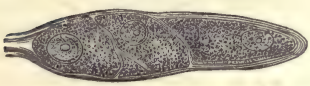

Fig. 285. Three quadrangular cells lying in a row.

It has been unwarrantably assumed that the cells of the sympathetic were uniformly smaller than those of the central nervous system; but it is easy to convince one's self of the error of this assertion, as cells of the largest size may readily be isolated from sympathetic ganglia. The consistence of these cells appears to be semi-fluid. After an alteration of form produced by the action of an external agent, they resume their original appearance on the cessation of the cause; a fact which would seem to indicate that they possess elasticity.

With the reagents at present employed we are able to distinguish in sympathetic nerve cells an envelope, a proper cell substance, a nucleus, and a nucleolus. The envelope or capsule of the ganglion cell is not to be looked upon as a cell membrane; for it is composed of connective tissue in which, nearly always, nuclei are embedded. The relation of this envelope of ganglion cells to the connective-tissue envelope of the ganglion has already been pointed out. Upon the inner surface of this envelope Fräntzel has discovered, in the sympathetic cells of several animals and of Man, a single layer of polygonal pavement epithelial cells. Occasionally the connective-tissue envelope exhibits concentric striation as well as nuclei.

Beale and Remak hold that these peculiar appearances of the connective-tissue envelope are produced by nerve fibres. J. Arnold has attempted to establish the view that a double envelope may be demonstrated around the sympathetic cells of the Frog; one a derivation of the perineurium of the nerve process, the other an extension of the neurilemma of the derived fibre.

When cells are rendered absolutely naked by preparation they exhibit no sign of a connective-tissue envelope.

As regards the substance of the nervous element, it consists of an homogeneous fundamental substance, in which are scattered fine granulations. The fibrillated structure attributed to ganglion cells by Max Schultze has not been satisfactorily seen by Arnold and Bidder.

Not infrequently there are seen in the cell substance a moderate number of delicate fibres proceeding from the nucleolus and nucleus. These fibres, of whose existence I myself together with Arnold and others have long been convinced, form a network, according to Arnold and Courvoisier. The assertion that this network is composed of fibres traversing the cell substance has been repeatedly contested. Kölliker believes only in the existence of a network upon the outer surface of the cell, a sort of sheath. But I, as well as Arnold, have observed that these fibres are apparent in cells which have been separated from their envelope. Sander ascribes the origin of this fibre network to rupture of the cell substance,—an opinion obviously originating in the study of badly handled nerve-cells. Fräntzel believes that the appearance of a fibre network may be produced by the limiting lines of the polygonal epithelial cells which line the interior of the cell envelope.

In sympathetic nerve-cells, and particularly well developed in those of Man, there exists a pigment of a yellow, or rusty brown color. As regards distribution, this usually granular pigment is sometimes scattered throughout the substance of the cell, sometimes accumulated in one part. The microchemical characters of this pigment have not been minutely investigated.

The nucleus of sympathetic nerve-cells is large, well defined from the cell substance, as may be particularly well demonstrated in chloride of gold preparations, in which the nucleus by its pale color contrasts with the violet-colored cell substance. It has been said that the nucleus is enclosed in a membrane; a well-marked double contour having been seen about it with certain modes of preparation. J. Arnold denies the existence of a special nucleus membrane; and neither have I been able to convince myself of its existence in the course of my numerous observations upon sympathetic cells and isolated nuclei. The substance of the nucleus is not homogeneous, but contains delicate fibres which spring from the nucleolus.

Remak long ago observed a fact confirmed recently by Guye, Schwalbe, and others, viz.: that in the sympathetic of Rabbits and of the Porpoise a majority of the cells presented double nuclei; an observation, the correctness of which may be confirmed by the simplest preparation from a sympathetic ganglion of the Rabbit. I have also often observed this double nucleus in the sympathetic cells of the Dog, Cat, Frog, and of Man. Bidder has described among the doubly nucleated cells of the sympathetic of the Rabbit, one in which the two nuclei were united by a fine fibre. I can fully confirm this observation of Bidder by my own investigations. These fine fibres, which I have thought it convenient to designate as nucleus-communication-threads (Kern-communicationsfäden), have been observed by me in nuclei separated from the cell substance, so that we

Fig. 286.

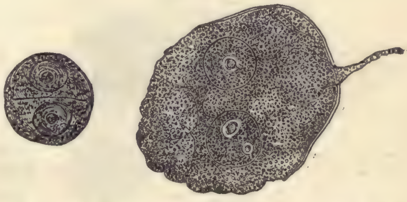

Fig. 286. Cells with two nuclei; one from the Rabbit, the other from the Frog.

may throw out the possible errors of confusion with folding of the cell envelope, coagulation of the cell substance, etc.

The position of the nucleus is very variable, both as regards its place in the fundamental substance, and as regards its relation to the second nucleus in those cases in which two nuclei exist. Sometimes the nucleus approximates to the outer layer of the cell substance, sometimes it is embedded in the midst of this mass. The variations in the position of double nuclei are even greater; they lie either wholly or nearly in the same plane, or in different planes near to or above one another, and separated by a distinct bridge of cell substance. Those instances in which the nuclei lie near one another in the same plane, offer peculiar facilities for observing the above described nucleus-communication-thread.

Nuclei as well as cells exhibit by no means insignificant variations in size. This cannot be overlooked in investigations made upon cells of ganglia taken from different animals. By passing in review the particularly numerous cells which exist in the nervous plexus ramifying upon the abdominal blood-vessels of the Frog, there may be seen in one place large cells with single large nuclei; in another a large cell with one large nucleus and a number of smaller ones (polar nuclei, Courvoisier); thirdly, large cells filled with a number of small nuclei; fourthly, small cells whose mass is nearly all occupied by the nucleus; fifthly, cells in which a number of small nuclei are embedded in a small quantity of cell substance. All these varieties may be observed in the Mammalia—Rabbits, Dogs, Cats; their frequency depending upon individual peculiarities, I intend to refer in detail to the signification of the above-described characters in another place.

The nucleolus is a structure which usually appears with extreme distinctness in nerve-cells. Especially in the strongly pigmented cells of the Adult does it show itself in brilliant contrast to the opaque substance of the nucleus and cell. Its position in the nucleus is a variable one; similar variations occurring here as have been described in relation to the position of the nucleus in the cell itself. The nucleolus is by no means rarely double, or numbers of nucleoli appear in the nucleus, either of uniform or of varying sizes. In the nucleolus itself other, but not constant bodies have been described by Beale, and the same had some time before been pointed out by Mauthner as present in the cells of the spinal cord. Svierczewski has described movements of nucleoli analogous to molecular movements, which may last a long time if the preparation be preserved from desiccation.

Fig. 287.

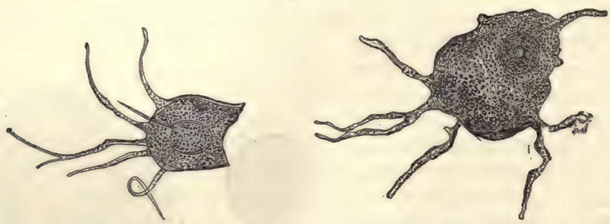

Fig. 287. **Two multipolar cells, one from a Child, the other from an Adult.**

An important character of sympathetic as well as of central nerve-cells is the existence of processes upon them. It was at one time believed that a certain number of cells without processes, apolar cells, were present in the sympathetic; but to-day the majority of histologists deny the existence of

apolar cells. It is certain that in the past there was too great tendency to conclude that because cells were often seen without processes, all cells did not have processes. But, as the facility with which processes are torn off in preparation, together with the relatively enormous mass of the cell body, tended to make observation difficult, it may be safely asserted that many instances of so-called absence of processes were due to the manipulation employed.

I must nevertheless maintain with Kölliker that cells do occur in the sympathetic in which no trace of a process can be observed; as well as no trace of laceration.

And the cuboidal cells already described as arranged in rows have as yet defied all efforts to demonstrate any processes on them, even in Bidder's latest researches. It would seem probable, however, that these cells are in a stage of development, and not exercising any functions.

The majority of sympathetic ganglion cells are unmistakably multipolar; the processes in part going to form nerve-fibres, in part constituting commissures between the cells themselves. In the latter case the fibres are as a rule very short; and the union of two ganglion cells by means of a short bridge is seldom seen, in all probability in consequence of the force used in making the preparation. A division of the processes into axis cylinder processes and branching processes, similar to that established by Deiters for the cells of the central nervous system, has been attempted. Schwalbe describes an instance in which an isolated cell from the sympathetic of the Cat showed the above distinction of processes into several branching processes and one axis cylinder process; and Bidder has recorded a similar observation. I have separated a cell from the cœliac ganglion of the Rabbit which showed with great distinctness besides several branching processes, two others which at a short distance from the cell became enveloped with myeline, and which were accordingly to be looked upon as axis cylinder processes. It consequently appears that the axis cylinder process is not always single. A peculiar sort of unipolar cell has been pointed out by Auerbach. Two cells lying in one sheath each send out from their opposite sides one process in an opposite direction. This form I, as well as Schweigger-Seidel, have not infrequently seen in various parts of the sympathetic.

Fig. 288.

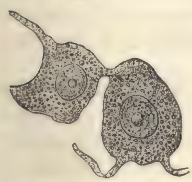

Fig. 288. Two cells united by a short commissure.

A great advance was made in our knowledge of the processes of sympathetic nerve-cells by the almost simultaneous discovery, by Beale and J. Arnold, of the fact that from the narrow end of the more or less bell-shaped nerve-cells of the sympathetic of the Frog two processes arise. One of these processes runs a direct course (*Geradefaser* of J. Arnold, *straight fibre* of Beale); the other winds itself spirally around the straight fibre (*Spiralfaser* of J. Arnold, *spiral fibre* of Beale). The straight as well as the spiral fibre lies inside of a sheath, usually nucleated, which is the direct continuation of the ganglion-cell envelope. On both fibres there may sometimes be seen nuclear bodies, such as have often been described as present upon non-medullated nerve-fibres. After pursuing in

Fig. 289.

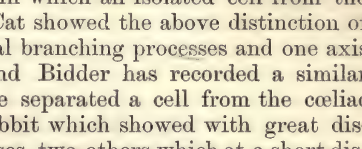

Fig. 289. Spiral fibre.

company a longer or shorter course, these fibres separate and continue their course in different directions. Both of these processes are held to be nervous, and the strongest evidence in favor of this view advanced by Arnold and Beale, lies in the fact that these observers have both seen the continuation of these processes with unmistakable dark-contoured fibres.

The relations of the spiral to the straight fibre offer great variations in regard to their size, and to the number of turns which the spiral fibre makes around the straight. Usually the straight fibre exceeds the spiral in thickness; though instances have been cited in which this proportion was not marked, or even was reversed. The spiral fibre is often multiple and is then of smaller diameter than when it exists singly. The number of windings is also very variable; sometimes the spiral arrangement is not at all evident, and the two fibres pursue a straight course side by side; while in other cases the spiral fibre winds corkscrew-wise around the straight. According to Beale, the spiral fibre is found principally on younger cells; and the number of turns of the spiral fibre increases in proportion to the age of the cell. My own researches in this matter have convinced me that while the spiral fibre is an exceedingly common attribute, it is not present in all sympathetic cells of the Frog. In this respect many individual peculiarities are met with, in regard to which it may be said that they probably depend upon the stages of development through which the cells happen to be passing.

Arnstein and Kollmann, Courvoisier, Guye, and Bidder substantially share Beale's and Arnold's view concerning the nature of both processes springing from nerve-cells; all claiming that they are nervous structures. Schwalbe is disposed to admit two sorts of spiral fibres, one of which, of nervous nature, springs from the cell substance, and makes few or no spiral turns around the straight fibre; a second which is to be considered as a thickening of the sheath and is developed from the fibre network of the cell. Krause considers the spiral fibre as an element essentially non-nervous in nature, and believes that either it represents an elastic fibre, or that its appearance is due to foldings of the neurilemma. The continuation of the spiral fibre into a dark-bordered nerve fibre has been satisfactorily ascertained by the above-named investigators as well as by Kölliker.

The spiral fibre, whose existence was first demonstrated in Frogs, is said by Courvoisier to be present in the higher Vertebrata. In the latter, however, the spiral windings of the fibre nearly disappear, and both fibres, straight and spiral, leaving one pole of a cell, pursue a more or less parallel course.

Since the discovery of the spiral fibre a confusion has arisen in the nomenclature of cells, because some authors (Arnold, Guye) call cells which give off two different fibres from one pole unipolar; while others (Beale, Kollmann and Arnstein) call them bipolar. Courvoisier proposes to call that part of the cell whence start the straight and the spiral fibres the holopole, twin-pole (Zwillingspol), or simply pole: each individual cell [fibre ?] would then have its origin in a hemipole. Cells with the two fibres springing from the same part Courvoisier would call geminous pole.

As regards the mode of origin of processes, histologists are divided into two parties, as has already been set forth in the third chapter of this work. While a number, Arnold, Fräntzel, Arnstein and Kollmann, and to a degree Bidder, assert that as observed by other investigators the fibre originates in the nucleus or nucleolus of the cell, others, as Kölliker and Schwalbe deny the existence of any connection between the processes and the nucleus or nucleolus. Courvoisier states that he has traced the straight fibre well

up to the nucleus, but he has not seen it terminate in the nucleus or nucleolus.

In the extremely large number of cells, mainly taken from the sympathetic of Mammalia, which I have studied with reference to this point, I have always seen the processes take their origin in the cell substance itself, the cell substance prolonging itself as it were into the process; and I have never observed any connection between the process and the nucleus or nucleolus. Occasionally, as stated by Schwalbe, the process at its point of entrance into the cell substance is seen to spread out like a brush. I have, furthermore, become convinced that there very commonly proceed toward processes of relatively large diameter which spring from the cell substance, a second system of delicate fibres originating in the nucleus and nucleolus. These delicate processes are none other than the already described nucleus and nucleolus fibrillæ. They run partly in the direction of the coarse processes and partly pursue an independent course; though it is very rarely that these delicate structures can be followed any distance beyond their point of exit from the cell substance. I have once seen such a fibrilla merge into a nerve fibre bearing myeline, and Beale has made mention of a similar observation. The origin of the straight fibre from the nucleolus, occasionally seen, cannot with certainty be referred to as the rule. In figure 290 is represented a cell from the sympathetic of the Frog in which the straight fibre, which exhibits a fibrillar structure under a high magnifying power, extends through the cell substance well into the nucleus; though here its mode of termination cannot be made out with certainty. I have no doubt but that under more favorable conditions it will become possible to discover the mode of union between the straight fibre and the nucleolus.

Fig. 290.

Fig. 290. Process running down to nucleus.

Similarly, unanimity of opinion concerning the mode of origin of the spiral fibre has not been reached. Arnold has advanced the view that the spiral fibre is developed from a network formed in the cell substance by the nucleolus fibrillæ. Beale believes that the spiral fibre originates in the more superficial layer of the cell substance, where there are usually accessory nuclei. Courvoisier in a first publication received Arnold's opinion, but in a second paper he does so with a certain reservation. This author describes, in addition, fibres which run from the network of nucleolus fibrillæ to neighboring cells, and these he calls commissural fibres. Arnstein and Kollmann have indeed observed fibres which converge from the cell substance toward the neck of the cell, and out of which network-like commingling the spiral fibre seemed to spring; they could not, however, actually see any union between this network and the nucleolus fibrillæ. Bidder, likewise, has not been able to convince himself of the occurrence of any connection between the spiral fibre and the fibre network whose existence he has maintained.

We can only conjecture what are the physiological attributes of these two kinds of processes. The question, which of the two shall be considered as the afferent fibre (originating in the cerebro-spinal axis), and which as the efferent (proceeding to the periphery), has been answered by Arnold, who ventures to call the straight fibre afferent and the spiral fibre efferent. Arnstein and Kollmann have expressed themselves similarly. In Courvoisier's experiments, in which he studied the degeneration following upon

section of the *rami communicantes*, the straight fibres first became sclerosed, then the cells, and lastly the spiral fibres. These results are likewise in favor of Arnold's view. Contrarily, Bidder, reasoning also from section experiments on the vagus of the Frog, considers the spiral fibre as afferent and the straight as efferent.

Beale has made a series of observations upon the progressive and retrograde evolution processes continually taking place in developing and developed individuals. His weightiest argument is based upon the simultaneous presence of cells of the most variable size, outline, number, and nature of processes, etc., in the sympathetic of the same individual. Beale admits three modalities of nerve-cell evolution. To the first belong cells consisting of a finely granular, nucleated mass similar to those of which the embryonic tissues are made up, and which are united to nerve-fibres. In the second place new cells may be produced by the division of a nerve-cell; and thirdly from the nuclei of nerve-cells. Beale's observations and deductions have received but little notice in Germany. Sander expresses himself positively against Beale's view, but, according to my experience in this matter, without reason. The various forms of ganglion cells described by Beale, and which appear to represent different stages of evolution, may easily (though not equally so in all individuals) be seen in the Frog; and as regards the ganglion cells of the Mammalia which I have studied, there occur evidences enough of the occurrence in them of evolution processes, such as the extremely variable size of the cell and its nucleus, the existence of disseminated finely granular masses with numerous scattered, brilliant bodies, cells without processes arranged in rows, etc. I mean, at some future time, to express my opinion in full upon these points, in another work. In the investigation of the sympathetic of the Frog, attention is especially drawn to accumulations of small bodies composed of a nucleus and a small amount of cell substance, and which are enveloped in a connective-tissue capsule. These nests of cells exist together in varying numbers, and these are again enclosed in a common capsule of connective tissue, more often nucleated. These nests are connected with nerve-fibres. The structures just described are found in very variable numbers in different individuals.

Fig. 291.

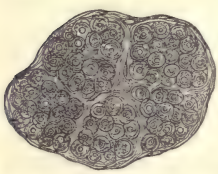

Fig. 291. A nest of cells.

Of the fibres of the sympathetic a number originate in the cerebro-spinal axis, others spring from sympathetic nerve-cells. In the *rami communicantes* we find fibres going from the spinal cord and the spinal ganglia, as well as some running in a contrary direction. The latter may pursue their way to the nervous centre, or to the periphery of the body by way of the spinal nerves. In the animals experimented upon by Courvoisier (Pigeon, Rabbit, Frog) the fibres of the *rami communicantes* were found to extend in the lateral cords of the sympathetic upward and downward in about equal proportions, but in the spinal nerves in the proportion of one-third centripetally, and two-thirds centrifugally. The fibres derived from the cerebro-spinal axis do not merely traverse the sympathetic ganglia, but, as recently demonstrated by Courvoisier by means of section experiments on the *rami communicantes*, and study of the consecutive degenerative processes, they are continuous with the substance of the cells composing the ganglia. After section of the *rami communicantes* the greater number of fibres in the stump of the sympathetic undergo degeneration; and the cells likewise exhibit the degenerative process in a peculiar manner described by Courvoisier. The spinal

stump suffers only a very limited sclerosis. According to Courvoisier there is a primary and a tertiary sclerosis in the sympathetic end of the *rami communicantes*, the latter being that which is transferred from the afferent to the efferent fibres of the cells.

As regards the nature of the fibres of the sympathetic, the opinion is now abandoned that the sympathetic nervous system is characterized by the presence of medullated nerve-fibres of small calibre similar to those which abound in the cerebro-spinal axis. In the sympathetic we find widely distributed small and medium-sized double-contoured fibres, as well as the various kinds of non-medullated fibres. The nature of these elements has been fully detailed in the third chapter of this work. The so-called transition fibres described by Courvoisier, such as appear to lose their myeline and again to acquire it, I have not rarely seen in the sympathetic of the Frog. Whether these fibres are produced by manipulations, as asserted by several authors, can only be determined by further researches.

As regards the distribution of the sympathetic nervous system, its principal relations, the course of its lateral cords, number of ganglia, etc., full details will be found in works on descriptive anatomy. Subsequently to the admirable researches of Remak and Bidder, sympathetic ganglion cells have been discovered in great number in nearly all the organs of vegetative and generative life.

In the circulatory apparatus, the heart encloses ganglion cells (Remak, Bidder: compare also seventh chapter of this work), and so do the blood-vessels (Beale, Lehmann) and the lymphatic glands (Shaffner). In the coccygeal gland, which according to the latest studies in this matter must be considered as an adjunct of the vascular system, Luschka has described ganglion cells which other observers have not, however, been able to see. Ganglion cells occur throughout the whole extent of the digestive tract, from the upper part of the œsophagus downward; lying in the submucous connective tissue (Remak, Meissner), and in the muscular coat (Auerbach). In the mucous membrane of the stomach, over the lamina muscularis mucosæ, Trütschel has very recently described a layer of large multipolar cells, which are united among themselves by means of processes, and which are of a nervous nature. In the glands attached to the digestive apparatus, the salivary glands and the pancreas, ganglion cells have been found in great number (Krause, Schlüter), and Manz has described them in the ducts of the liver and pancreas.

In the respiratory apparatus nervous elements are met with in the lungs, and in the tissues of the larynx and trachea. The genito-urinary tract contains ganglion cells, in the bladder and ureters, in the testicles, upon the prostate, in the corpora cavernosa (Lovén), in the uterus and in the vagina. Ganglion cells have been met with in the so-called ductless glands, as the supra-renal capsules; and recently Fleischl has described them in the thymus-like organ of the Frog.

The special senses exhibit sympathetic nervous elements in the lachrymal glands attached to the optic apparatus, and in the ciliary muscle (H. Müller). In the striated muscular fibres of the iris of the Fowl, Von Hüttenbrenner has observed cells which he is inclined to look upon as nerve-cells. For a minute description of the distribution of ganglion cells in the various organs of the body, reference may be made to various portions of this work.

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13. V. HÜTTENBRENNER, Ueber eigenthümliche Zellen in der Iris des Huhnes. Sitzb. der k. k. Akad. zu Wien. Jahrg. 1869. Bd. LX.
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17. J. SANDER, Die Spiralfasern im Sympathicus des Frosches. Archiv. von REICHERT und DU BOIS-REYMOND, 1866, III. Heft. p. 398.
18. SCHWALBE, Ueber den Bau der Spinalganglien nebst Bemerkungen über die sympathischen Ganglienzellen. Archiv für mikroskop. Anat. Bd. IV.
19. SVIERCZEWSKI, Zur Physiologie des Kernes und Kernkörperchens der Nervenzellen des Sympathicus. Centralblatt für die medicinischen Wissenschaften, 1869, No. 41.
20. TRÜTSCHEL, Ueber die Endigung der Nerven in der Schleimhaut des Magens. Centralblatt für die med. Wissenschaft, 1870, No. 8.

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CHAPTER XXXIV.

THE ORGANS OF TASTE.

By TH. W. ENGELMANN,

IN UTRECHT.

A. The Organs of Taste in Man and Mammals.

Already for many years past physiology has pointed out the most prominent spots in Man where the peripheral end-apparatuses of the nerves of taste must lie: these are the upper surface of the root (especially the papillæ circumvallatæ), the edges and tip of the tongue, probably also the anterior portion of the soft palate. Observations and experiments have rendered it furthermore probable that there are different kinds of end-apparatuses, and that these are not uniformly distributed over the regions where the sense of taste exists. Still it is only quite recently that microscopic anatomy has acquainted us with organs in Mammals which we could justly designate as the end-apparatuses of the nerves of taste. Chr. Lovén and G. Schwalbe discovered, independently of each other, in the laminated pavement epithelium which clothes the papillæ circumvallatæ in the tongue of Mammals, numerous small microscopic bud-like groups of cells which stood with their ends upon the twigs of the Nervus glossopharyngeus; Lovén called them *taste-buds* (Geschmacksknospen) or *taste-bulbs* (Geschmackszwiebeln), while Schwalbe termed them *taste-beakers.*

These organs have now been demonstrated in Man, the Dog, Cat, Cow, Sheep, Roe, Horse, Pig, Hare, Rabbit, Guinea-pig, Rat, and Mouse.

The taste-buds (fig. 292) occupy cavities in the epithelium of the mucous membrane of the tongue, and fit them perfectly at every point. The shape

Fig. 292.

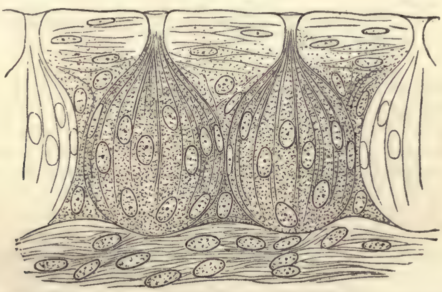

Fig. 292. Taste-buds from the lateral organ of taste in the Rabbit. $\frac{450}{1}$.

of these cavities resembles a flask with rounded belly. The bottom of the flask rests upon the connective-tissue surface of the Mucosa; the slender

and generally short neck of the flask pierces the horny layer of the epithelium and terminates at the surface with a round opening—*taste-pore*, as we shall call it. The longitudinal diameter of the taste-buds—which always exceeds the greatest transverse diameter—varies in Man from 0.077 to 0.081 mm.; the greatest transverse diameter is about 0.0396 mm.; the width of the taste-pore is from 0.0027 to 0.0045 mm. (Schwalbe).

The taste-buds differ a little in form in the different animals. In some (Ox, Pig) they are slender, their length being almost three times as great as their breadth; while in others (Rabbit, Roe) they are more compact, the length exceeding but little the breadth. The most slender, moreover, are usually the largest. The size also varies somewhat, not alone in the same species, but even in the same individual. Larger and smaller specimens often occur side by side, without any regularity in their arrangement. I subjoin a few of the dimensions; they were taken mostly from Schwalbe's statements:

	Dog.	Ox.	Pig.	Rabbit.
Longitudinal diam. of the buds in millimetres..............	0.072	0.172	0.055–0.130	0.0450–0.070
Greatest transverse diam. in millimetres..................	0.0306	0.048	0.020–0.052	0.03–0.045
Breadth of taste-pores in millimetres....................	0.0045	0.002–0.009	0.0027	0.003–0.0045

In the mucous membrane of the tongue, the chief places where the taste-buds lie are the lateral slopes of the papillæ circumvallatæ. Here they form a broad girdle around the papilla, to the number sometimes of several hundred. They are also found, though not so often, and then only solitary examples, on the papillæ fungiformes. In the Rabbit and Hare, moreover, there exists at the root of the tongue, on both sides, a large oval prominence, which is subdivided by some ten to fourteen deep, parallel, transverse furrows into narrow ridges (taste-ridges) that conceal thousands of taste-buds. If we make an exception of the fungiform papillæ, which now and then carry taste-buds on their free surface, the organs of taste may be said to occur always in parts of the mucous membrane of the tongue which are particularly protected, *i. e.*, in furrows and at the bottom of crevices. Thus, for instance, in the papillæ circumvallatæ they are never to be found in the epithelium of the plateau, but in the lateral slopes of the papilla, which are protected by the surrounding circular wall; the same is true of the lateral organs of taste in the Rabbit, where the buds never occur along the summit of the ridges, but always in their sloping sides.

Structure of the taste-papillæ and taste-ridges. *The papillæ circumvallatæ* (fig. 293), whose numerous varying forms we shall not treat of here, consist of a connective-tissue body, having in general the form of a truncated cone, and covered with a laminated pavement epithelium. "At its summit the papillary body is covered with a large number of conical, filiform, and occasionally bifurcating secondary papillæ, which at the edge of the upper surface and along the side are supplanted by vertical —*i. e.* parallel with the axis of the papilla—low ridges with intervening groove-shaped furrows." "The depressions between all these elevations are completely filled in by the epithelium, so that the surface of the papilla presents everywhere a perfectly smooth appearance, without even a trace of the subjacent unevennesses." (Lovén.) On the upper surface and on those parts of the sides of the papilla which are not protected by the circular wall, the layer of epithelium is much thicker than on the protected portions of the sides of the papilla; but even in the former of these localities it is very much thinner than throughout the general surface of the tongue. The epithelial layer is also thinner on the outer wall of the circular trench. The taste-buds are

situated in the thin epithelium covering the sides of the papilla; in fact they usually form there a zone which reaches from the bottom of the trench up nearly to the point where the external surface of the papilla is no longer protected by the wall (Schwalbe). The zone encircles the papilla with the circular wall. If the trench is deep (Sheep, Pig), then the zone is broad; if it is shallow (Horse), the zone will be narrow. In Man, however, the upper half of the side walls of the papilla is generally free from taste-buds, even where the surrounding wall extends high up (Schwalbe). As the taste-buds usually stand close together (the closest in Man, according to Schwalbe, where they almost touch each other), their number in a single papilla is very great. Schwalbe estimates them in the Sheep—in a papilla of medium size—at 480, in the Cow at 1,760; in the Pig, where there are but two circumvallate papillæ, each possesses about 4,760. This would give for all the papillæ an aggregate of 9,600 in the Sheep, 35,200 in the Cow, in the Pig 9,520. In Man and the Dog (Schwalbe), and also in Rats and Rabbits (Lovén), a few scattering taste-buds are also found on that side of the circular wall which faces the papilla. With reference to the relations of the nerves, that enter the papillæ, to the apparatuses of taste, see farther on.

Fig. 293.

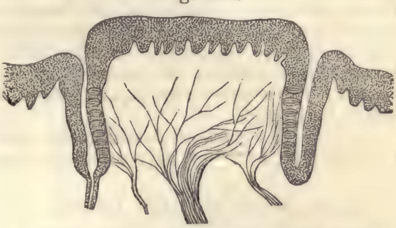

Fig. 293. Section of a papilla circumvallata from the Calf, showing the arrangement of the taste-buds. $\frac{25}{1}$.

The *papillæ fungiformes*, among which are often found forms of transition to the papillæ circumvallatæ, possess also materially the same structure as the latter. The mantle, however, of taste-buds is not to be found in them. Nevertheless Lovén discovered (in the Calf) scattering taste-beakers on their free upper surface, between the secondary papillæ. In the Rabbit and Rat he found them in every papilla fungiformis; in the small ones, though, there was only a single specimen in each. Schwalbe at first doubted their existence in the fungiform papillæ, but afterwards met with them himself, in the Pig in particular. I have also seen them in the Mouse and Cat, in vertical sections. Their occurrence in the fungiform papillæ, according to Lovén, is much rarer in Man, the Dog and the Calf, than in the aforementioned animals.

The two *lateral organs of taste* of the Rabbit and Hare, of which mention was made above, seem hitherto, in spite of their large size, to have escaped observation;* and yet they are organs of taste *par excellence*. Each of them consists of a flattened oval eminence lying on one side of the base of the tongue and traversed on its surface by from 10 to 14 parallel transverse furrows. In the Rabbit the organ measures about 5–6 mm. in length (from before backwards), and 2.5–3.5 mm. in breadth. In the Hare it is somewhat larger. Fig. 294 represents a portion of a vertical section which has been carried through the centre of the organ at right angles to the direction of the

Fig. 294.

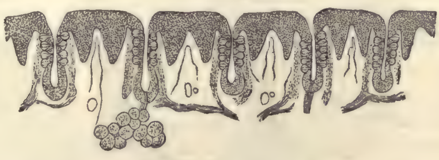

Fig. 294. Transverse section of several taste-ridges, from the lateral organ of taste of the Rabbit. $\frac{25}{1}$.

* No mention is made of them in the anatomy of the Rabbit by W. Krause. The lateral organs of taste, however, were also discovered and described by Hans Von Wyss: H. von Wyss, Ueber ein neues Geschmacksorgan auf der Zunge des Kaninchens. *Centralblatt f. d. med. Wissensch.* 1869. No. 35. p. 548. The detailed description is given in the *Archiv für mikr. Anatomie*, 1870. The description given by Von Wyss agrees perfectly with mine, which, by the way, was handed in for publication already in the summer of 1869.

furrows. Four entire taste-ridges and the halves of two others are seen in transverse section. The ridges are separated from each other by deep clefts, at the bottom of which in some instances acinous glands disembogue. In each of these small ridges there can be distinguished a connective-tissue body, which breaks up into three secondary ridges. The middle one of these is broader than the other two. The connective-tissue body is covered by a laminated pavement epithelium, which is much thicker on top than at the sides of the ridge, and completely fills up the furrows between the smaller secondary ridges. In the sides of each ridge, throughout its entire length, lie the taste-buds. They form here a broad band, the lower edge of which extends down a little below the middle of the furrow, while its upper border reaches up to the opening of the fissure above. The taste-buds stand so close together as almost to touch (figs. 292 and 295). In the Rabbit the band is usually four rows deep. Each row contains in its entire length perhaps 80 buds. For each taste-ridge, therefore, the approximate sum would be 620 buds; or, for both organs of taste together—reckoning 12 ridges to each—the entire number of taste-buds would be 14,880.

According to Schwalbe's statements, two similar organs are to be found in the Pig; they contain, however, only scattering taste-buds.

As already stated, the taste-buds (fig. 292) lie in flask-shaped cavities of the epithelium, filling them completely. The walls of these flask-shaped spaces, with the exception of the bottom, which rests upon the connective tissue of the mucous membrane, are composed of the epithelial cells. Around the belly of the flask the epithelium consists of cells of various shapes, which possess the peculiar characteristics of the Rete Malpighii, *i. e.*, a finely granular protoplasma, a comparatively large nucleus, and an indistinct membrane. The innermost of these cells, which are glued, so to speak, to the wall of the flask-shaped space, are concavo-convex in form, like fragments of a watch-glass; when seen in transverse section (fig. 295) they are sickle-shaped. In the neighborhood of the neck of the flask and near its opening, the taste-pore, the epithelium presents the same peculiarities as the flattened epithelium of the buccal mucous membrane: a flattened form,

Fig. 295.

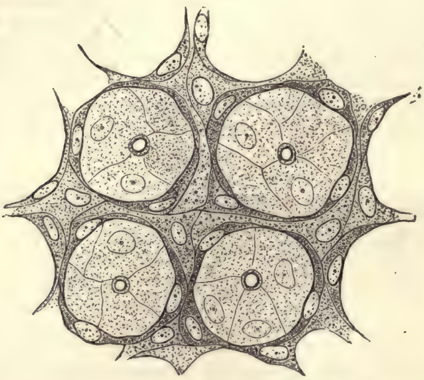

Fig. 295. Upper half of the epithelial support of the taste-buds. The observer is looking from the under side into four cavities, out of which the buds have fallen. At the bottom of each the taste-pore is visible. From the lateral organ of taste of the Rabbit. $\frac{450}{1}$.

thick membrane, homogeneous contents, and flattened nucleus. In those regions where taste-buds occur, the horny layer measures as a rule only 0.01 to 0.02 mm. in thickness, and passes, below, without any sharply-

drawn boundary into the stratum Malpighii. The margin of the taste-pore is usually formed by the union of several cells, though sometimes only one cell will enter into its formation; in that case the cell will simply be perforated by a round hole in any part of its substance. At the margin of the opening, moreover, there is often a circular thickening (fig. 295.)

Figs. 292, 295, and 296, all of which were taken from preparations of taste-ridges in the Rabbit, are intended to give additional clearness to the subject. Fig. 292 represents a perpendicular section through the entire thickness of the taste epithelium; the taste-buds are still in their flask-shaped cavities. Fig. 295 represents a view from below of the upper half of the epithelial support that surrounds the spaces for the taste-buds. This half of the epithelium, in the course of the manipulation, became detached from the deeper layer as a continuous plate. The taste-buds themselves together with the lower half of the epithelium remain attached to the mucous membrane. In the figure the observer is looking from below into the opened empty cavities, at the bottom of each of which he will recognize the sharply outlined taste-pore, encircled by a thickened ring. Fig. 296 completes fig. 295: it represents a view from above of a taste-bud which still is attached to the mucous membrane, and is surrounded by the lower half of the epithelial support.

Fig. 296.

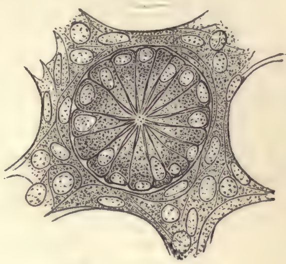

Fig. 296. A taste-bud laid bare by the removal of the upper half of the surrounding epithelial support; viewed directly from above. From the lateral organ of taste of the Rabbit. $\frac{450}{1}$.

The *taste-buds* or *taste-beakers* (fig. 297), which occupy the above-mentioned cavities, consist each of a number—from 15 to 30, according to the size of the buds—of long, thin cells, arranged in a similar manner to the leaves of a bud. These cells, closely packed together, surround the axis of the bud in several rows. Those on the outside lie in exact contact with the walls of the cavity and must therefore be correspondingly curved (the concave side looking inwards); the form of the inner cells becomes straighter the nearer they approach the axis. All taste-buds appear to be composed of at least two fundamentally different kinds of cells; in the first place, of such as do not essentially differ from epithelial cells and are not connected with nerves; secondly, of peculiar bodies, of a higher degree of organization, which are probably connected with nerve-fibres and are to be looked upon as the real *taste-cells.* The former, which with Lovén and Schwalbe we may call *cover-cells,* constitute the outer layers of the bud and are the most numerous of the two; the latter lie, as it appears, chiefly near the axis of the bud.

Fig. 297.

Fig 297. Isolated taste-buds from the lateral organ of taste of the Rabbit. $\frac{600}{1}$.

The *cover-cells* (fig. 298) are long, rather narrow, generally somewhat spindle-shaped elements, which contain midway between both ends—sometimes nearer one end—an ellipsoidal, bladder-like nucleus. They consist of a clear protoplasma containing almost no granules, and they apparently have no membrane. Towards the taste-pore they gradually come to

a sharp point, while at the lower extremity they either diminish but little in size, resting firmly with a pretty broad base upon the connective-tissue surface of the mucous membrane, or they gradually taper down into one or more processes (sometimes two-cleft), which often do not reach the surface of the mucous membrane at all.

Fig. 298.

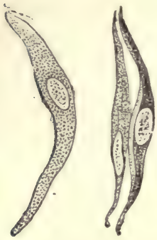

Fig. 298. Isolated cover-cells from the taste-buds of the Rabbit. $\frac{600}{1}$.

In specimens from the Sheep, that had been treated with perosmic acid, Schwalbe found at the apex of the bud a circle of delicate short hairs whose ends converged inwards and whose point of origin, as he supposed, was the end of the cover-cells. These cilia did not dissolve in caustic potassa even after a prolonged stay in the fluid; after the isolation of the buds, however, in solutions of chromic acid, the cilia could no longer distinctly be made out. In other animals and in Man their existence has not been satisfactorily demonstrated. Lovén and Schwalbe found that cover-cells, whose lower ends were prolonged into narrow processes, could be isolated with greatest ease in the taste-buds of Man and also of the Calf. The processes were never found to be varicose, although they often presented a knob-like swelling at their extremity. Some of the cover-cells drawn by Lovén (l. i. cit. Fig. 6, *e. g.*, also *h. i. j.*), remind one of the forked cells of the Frog, to be described hereafter, and very probably were, like these, true taste-cells of a peculiar shape.

The length of the cover-cells depends as a rule on the length of the taste-buds, and varies within about the same limits as these, *i. e.*, in the Rabbit, for instance, between 0.045 and 0.065 mm. Moreover, in the same bud the cover-cells will be found to vary in size: the largest and broadest, and at the same time the flattest, constituting as a rule the outermost layer. The inner cells are shorter and more cylindrical.

The *taste-cells* (fig. 299 *a* and *b*) are long, thin, almost always homogeneous and strongly refractive elements. Each consists of an ellipsoidal body, which is prolonged at its upper pole into a tolerably broad, at its lower pole into a narrow process. The body consists of a bladder-like nucleus which is sur-

Fig. 299.

Fig. 299. *a*, isolated taste-cells from the lateral organs of the Rabbit. $\frac{600}{1}$. *b*, a taste-cell and two cover-cells isolated in a connected condition; from the same source. $\frac{600}{1}$.

rounded by a thin layer of homogenous substance—"protoplasma." In the Rabbit the broader upper (peripheral) process is almost cylindrical, growing a trifle narrower towards the point; as a rule it is $2\frac{1}{2}$ to 3 times as long, and at its middle point about half as broad as the nucleus of

the cell. The termination of this process is usually of a blunted conical shape, and is prolonged on one side into a delicate short hair or rod, which stands perpendicularly to the blunted end (fig. 299, *a*). The ends of these delicate hairs seem, in the normal condition, scarcely to reach the level of the taste-pore. The lower (central) process is thin, cylindrical, and already, at a very short distance from the nucleus, about three times as narrow as the above-described peripheral process. At a distance of from 0.006 to 0.0012 mm. from the nucleus it usually subdivides into two only slightly thinner branches, which extend down to the surface of the mucous membrane. Before this takes place, however, the branches not infrequently again subdivide, once or several times, in rapid succession. The chemical reaction of the central process seems to be the same as that of nerve fibrillæ.

In the Calf, Lovén found the taste-cells differently constructed: the peripheral process was cylindrical, staff-shaped, but carried no hair at its extremity. The central process was a long, delicate thread, studded with varicose swellings and what appeared to be the short broken ends of lateral twigs. In Man, Lovén found the peripheral process shorter and somewhat pointed at the end; in all other respects, however, it was the same as in the Calf.

Schwalbe would distinguish, in Man and the Sheep, two kinds of taste-cells: *needle-cells and staff-cells* (Stiftchenzellen und Stabzellen). In the former, which are the most numerous, the diminished end of the broader peripheral process terminates "in a narrow, brilliant needle whose upper end appears to have been cut off abruptly." In taste-buds that had been isolated by the aid of perosmic acid the needles sometimes projected a distance of 0.0072 mm. beyond the apex of the bud. The central process is filiform and sometimes varicose. Schwalbe was unable to find the lateral twigs described by Lovén. In the staff-cells the peripheral process is "shorter, of uniform breadth, and terminates abruptly without any needle. The central process, however, can scarcely be distinguished from that of the ordinary taste-cells."

It is still unknown whether in different parts of the tongue various forms of taste-cells occur which are capable of transmitting different taste-sensations. It is equally unknown whether in a single taste-bud only one or several varieties of taste-cells may occur.

The Nerves.—We possess very little information concerning the connection between the nerve-fibres and the elements of the taste-buds. It is known that small branches of the N. glossopharyngeus, consisting chiefly of slender medullated fibres, proceed towards the papillæ circumvallatæ and ramify throughout their substance. A short distance before their entrance into the papilla these small branches will be found to contain—as does also the main trunk of the Glossopharyngeus (Remak)—microscopically small groups of ganglion cells. Immediately beneath the papilla they form, especially in the Sheep, a richly developed plexus (Schwalbe). From this plexus one or more larger bundles penetrate centrally into the papilla, and a few bundles will often enter it from the side; once within the papilla they subdivide into numerous fine intercrossing and intertwining twigs, which radiate towards the epithelium. As a rule these twigs contain many more pale than darkly-outlined fibres. Most of the bundles of nerve-fibres direct their course towards where the taste-buds lie, and then ramify throughout the thin stratum, rich in nuclei, immediately upon which the buds rest. In this stratum, according to Schwalbe, the nerves consist—apart from a few scattering medullated fibres—of delicate bundles of fibrillæ, each of which is surrounded by a nucleated sheath which is rendered pale by the addition of acetic acid. These bundles, by repeated subdivision, break up into finer and finer twigs, from which finally proceed delicate pale fibres that resemble very strongly the processes of the taste-cells and form a second plexus immediately beneath the epithelium. It is highly probable that these finest fibrils are continuous with the central processes of the taste-cells. After brushing off

the epithelium from chromic acid preparations, Schwalbe sometimes saw entirely similar fibrils projecting above the surface of the mucous membrane.

Quite the same relations of the nerves are to be seen in the taste-ridges of the Rabbit and Hare as in the circumvallate papillæ. The numerous and rather thick branches of the Glossopharyngeus, which ramify beneath the taste-ridges, contain pretty large microscopic collections of ganglion cells. In one of them I counted over thirty cells. They were almost spherical in shape, averaging about 0.05 mm. in diameter, and seemed to be connected with nerve-fibres only at one pole. Very numerous and still quite thick bundles of pale fibres proceed from the larger nerve-branches to the zones of taste-buds. At all the points above which these buds are situated, but at none others, the mucous membrane is extremely rich in nuclei (see fig. 294, where the condition is indicated by dots; also fig. 292). In this nucleated layer are found an extraordinarily large number of very delicate, pale nerve fibrils, which in thickness, form, power to refract the light, and also, as it appears, in their chemical reaction agree with the central processes of the taste-cells. They may be followed not infrequently as far as to the base of a taste-bud, and then are lost to view.

We may mention here, by way of an appendix, the descriptions given by Szabadföldy and Letzerich of the mode of termination of the nerves of taste in Mammals. According to the former, they terminate in pear-shaped bodies, which lie concealed in the connective tissue of the mucous membrane; consequently they never can come into direct contact with the substances which pass through the cavity of the mouth. The consciousness, however, of the sensations of taste is appreciated in much less time than it would take for any known solution to diffuse itself through the thick epithelial layer; hence it naturally follows that the organs described are not really organs of taste, as Szabadföldy would have us believe. No one else, however, has since been able to find them. The statements of Letzerich have hitherto met with equally little confirmation. According to him, the nerves of taste, in all the papillæ of the Cat, Cow, and Weasel, terminate in "pretty large, flat, bladder-like bodies, whose investing membranes are structureless and studded with large nuclei. These bladders lie above the plexus which is situated in the papillary and lingual mucous membrane." They possess two kinds of processes. One kind are nipple-shaped: they are directed towards the connective tissue of the mucous membrane, and are connected with darkly-outlined nerves, which become pale at the point of connection. The axis cylinders traverse the protoplasmic contents of these nipple-shaped processes and subdivide dichotomously over the inner surface of the bladder. "Upon these subdivisions are seated small, shining, prismatic bodies (nerve terminal bodies) which resemble strongly the rods of the retina. The bladders themselves are filled with hyaline, feebly granular masses." The second kind of processes are tubular diverticula of the membrane of the bladder, which project toward the surface of the tongue, as far as into the horny layer of epithelium. Their ends always remain covered by a layer, however thin, of epithelial cells. Letzerich did not meet with the organs of taste discovered by Lovén and Schwalbe.

B. Organs of Taste in Amphibia.

While the organs of taste in Birds and Reptiles are unknown, they have been for a long time well understood in the Batrachia (Rana esculenta and temporaria, Hyla arborea). In Frogs the end-organs of the nerves of taste also consist of microscopically small groups of characteristic epithelial formations, which lie in cavities of the epithelium that covers the mucous membrane of the tongue and soft palate. The form, however, of these organs does not resemble a flask or bud, as in Mammals, but is more like that of a disc. Inasmuch as they correspond perfectly to the taste-buds, we shall call them *taste-discs*. They may be counted by hundreds, and are distributed pretty uniformly over the upper surface and borders of the tongue; each sits upon a broad, somewhat cylindrical papilla (taste-papilla, papilla fungiformis). Numerous taste-discs are found even in the epithelium covering the smooth, non-papillate surface of the soft palate, but they rise, either

not at all or only slightly, above the level of the surrounding epithelium; in this locality they require further investigation.

MINUTE STRUCTURE OF THE TASTE PAPILLÆ IN THE FROG (R. esculenta and temporaria).—These papillæ consist of a connective-tissue body, covered with epithelium, whose general shape resembles a low cylinder or a truncated cone. Upon the circular or elliptical end-surface of the papilla sits the taste-disk, surrounded by a narrow girdle of ciliated cells. The taste-disk itself is composed of peculiar cells and cell-like bodies. The side surfaces of the papilla are covered with a simple, non-ciliated cylindrical epithelium.

The larger lower portion of the body of the papilla consists of a rather loosely-woven connective tissue, in which loops of capillary vessels, the branching ends of muscular fibres, and a bundle of darkly-outlined nerves lie embedded. The upper portion is a solid disk, 0.01–0.015 mm. thick, of a dense, non-nucleated connective tissue; to it we may give the name of *nerve-cushion.* It constitutes the bed upon which rests the taste-disk.

From five to ten darkly-outlined nerve fibres come up from below into the papilla, and remain in its axis, rarely giving off any branches until they reach the under surface of the nerve-cushion. On their entrance into the latter, or just before, they become somewhat narrowed, and suddenly lose their medullary substance and neurilemma. Thereupon the nerve fibres—which have now grown very thin (circa 0.002 mm.) and pale—at once commence to subdivide, and, by repeated dichotomous branching, form a delicate, close nervous network, which spreads itself out in the lower half of the nerve-cushion in nearly a horizontal direction. From this web numerous delicate twigs (fig. 300) shoot upwards, in a straight or oblique direction, as far as to the surface of the nerve-cushion; they, too, are wont to give off branches. At this point they become connected with certain elements of the taste-disk which we shall soon describe.

The bundles of nerves which enter the P. fungiformes, come from the N. glossopharyngeus. The small papillæ of the Frog's tongue, which are covered with ordinary epithelium, seem, as Billroth has already mentioned, to be unprovided with nerves. The nerve-cushion is firmly attached below to the connective-tissue body of the papilla, while at the sides it terminates with smooth and sharp limits; the cushion itself consists of a very firm connective tissue, indistinctly fibrillated, which swells up less in dilute acids and alkalies than ordinary fibrillated connective tissue. Key considered the nerve-cushion as an enormous enlargement of the neurilemma and called it the nerve-shell.

The pale nerve fibres, into which the darkly-outlined fibres resolve themselves on entering the nerve-cushion, were first discovered here by Key. The numerous dichotomous subdivisions of the nerve fibres seem, however, to have escaped his notice, for he describes them as breaking up rather into pencils of the most delicate varicose branches. Our own description was given from fresh preparations that had been laid in serum and diluted glycerine.

The *taste-disks* are elliptical or circular, sharply outlined epithelial plates, whose transverse diameter measures about 0.15–0.35 mm. and their thickness 0.04–0.05 mm. Their under surface is firmly attached to the nerve-cushion, while the upper comprises the entire end-surface of the papilla. The "*nerve-epithelium,*" of which the entire mass of the taste-disk is composed, may be distinguished from the ordinary cylindrical and ciliated epithelium, which covers the remaining surface of the papilla, by the circumstance that optically it is almost homogeneous and very transparent; by transmitted light, therefore, it has a very clear appearance. When seen, moreover, in thick layers, it presents a pale yellow tinge.

It is more firmly adherent to the papilla than the surrounding epithelium. The cells composing the taste-disks are also more firmly and intimately united together than those of the ordinary epithelium.

Leydig was the first to call attention to the fact that the epithelium which covers the end-surfaces of the papillæ fungiformes, differs from the rest of the epithelium. Later observers have all, with the exception of Fixsen, confirmed this. Then Billroth and, in particular, Ernst Axel Key, furnished the minute details concerning the nerve-epithelium.

The taste-disks of the Frog are made up of several kinds of cells; but of these the forked cells are very probably the only ones that are connected with nerve-fibres. Two other kinds of cells, the broad cup-cells and the narrow cylinder cells, seem to possess a more indifferent nature, like the cover-cells in the taste-beakers. These three kinds of cells are distributed throughout the taste-disk in such a manner that the bodies of the cup-cells, of which there is only a single layer, constitute the outer portion of the disk, while their central processes together with the bodies of the cylinder and forked cells form the under layer of the epithelium. The last-mentioned cells send their peripheral processes in a straight direction between the bodies of the cup-cells as far outwards as to the surface of the taste-disk (figs. 300 and 302).

Fig. 300.

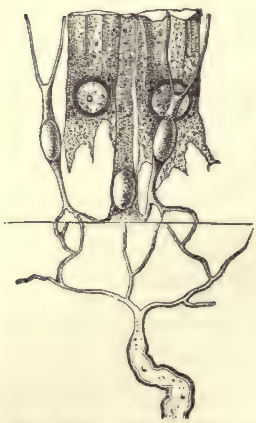

Fig. 300. Termination of the nerves of taste in the Frog. Ramifications of a nerve fibre in the nerve-cushion, from a glycerine preparation. Group of two cup-cells, one cylinder, and two forked cells from a chromic acid and glycerine preparation. $\frac{600}{1}$.

The *cup-cells*, of which there are several hundred in each of the large papillæ, are cylindrical bodies which by mutual pressure are usually converted into five- or six-sided prisms. The body of the cell measures from 0.02 to 0.024 mm. in length, and 0.01 mm. in breadth; in its lower third lies a vesicular nucleus. Below the nucleus the body of the cell becomes somewhat smaller and terminates in a protoplasmic process of irregular shape. The body of the cell is enveloped by a firm, cup-like membrane which has a broad opening on top. This cup is filled to the edge with a transparent protoplasma, which appears to be almost homogeneous. The process of the cell also consists of an almost homogeneous protoplasma. The membrane, which below has been steadily growing thinner, finally ceases to be demonstrable over the process of the cell. The processes of neighboring cup-cells form, by mutual contact, and probably also by fusion, a meshwork of protoplasmic substance in the under layer of the epithelium.

The cup-cells were described by Key as modified epithelial cells. Their dimensions remain pretty constant. Through the action of many reagents—*e. g.* a prolonged stay in iodized serum—the protoplasma will sometimes escape from the body of the cell, leaving the nucleus, however, behind. The thick cell-membrane is thereby thrown into deep longitudinal folds. By acids—acetic acid, for instance, and also perosmic acid—the protoplasma of the cup-cells is rendered much more opaque than that of the ordinary epithelial cells of the surface of the tongue. These cells must not in any way be confounded with the so-called beaker cells.

The *cylinder-cells*, several hundred of which are seated on every papilla, consist each of an ellipsoidal body, measuring about 0.006 mm. in

length and 0.004 mm. in breadth, and seated directly upon the nerve-cushion, in the deepest layer of the epithelium. Towards the periphery the body becomes lengthened out into a cylindrical, usually straight process, about 0.032 mm. long and 0.002 mm. thick, which extends even to the outer surface of the epithelium. The body consists of a thin mantle of protoplasma enveloping an ellipsoidal nucleus. The substance of the long cylindrical process is composed of a very finely granular protoplasma, which appears to be surrounded by a thin membrane, open at the top. The protoplasma of the cell-body spreads itself out—usually in the form of several short processes—horizontally over the surface of the nerve-cushion. These processes never present the appearance of nerve fibres.

Key's "staff-cells" undoubtedly were to a large extent cylindrical cells (see especially figs. 5, 7, 10, and 11, *b*, *c*, *g*, of his work, mentioned in the appended bibliography). He confounded them, nevertheless, with the forked cells, which we are soon to describe, and of which only mutilated specimens seem to have come under his observation. That the long process of the cylindrical cells is enveloped by a membrane, open at the top, I conclude from the circumstance that occasionally, in iodized serum preparations, for instance, the membrane gradually becomes flattened until it displays the appearance of a band, while at the same time small lumps of protoplasma push their way out from the top.

The *forked cells* (figs. 300 and 301), which are probably twice as numerous as the cup-cells, consist, like the taste-cells in Mammals, of a body together with long, thin processes. The body has the form of an elongated ellipsoid, its greatest diameter measuring from 0.006–0.008 mm. and its smallest from 0.003–0.004 mm.; it is almost entirely filled with a vesicle-like nucleus and central nucleolus. The processes are given off from the peripheral and central poles of the body.

The peripheral process is generally forked, and from 0.021 to 0.030 mm. long. Its ends extend to the free surface of the epithelium. Here, too, as in a fork, we can distinguish a handle and prongs. The cylindrical handle, which averages from 0.0015–0.002 mm. in thickness, never measures more than 0.008 mm. in length; it may even be altogether wanting. The shorter it is, the longer will be the prongs that project from it, and *vice versâ*. The handle subdivides into two or, more rarely, three prongs, which in turn sometimes form secondary forks. A third prong is also occasionally given off from the side of the handle. The ends of all the prongs lie in the same plane—that of the surface of the epithelium. The prongs are small cylindrical rods, not exceeding 0.001 mm. in thickness, which in physical characteristics and chemical reaction resemble very closely the pale nerve fibres.

Fig. 301.

Fig. 301. Isolated forked cells from the Frog (R. temporaria). $\frac{600}{1}$.

From the central pole of each forked cell is given off a single cylindrical process (rarely two or three finer ones) which averages 0.0015 mm. in thickness, and, at a distance usually of 0.006 mm.—at the farthest 0.025 mm.—from the pole, subdivides into two branches. From these branches, by repeated subdivision, proceed smaller, very slender branches, of the se-

cond and third order, which coincide in every particular with the pale nerve fibres that appear on the upper surface of the nerve-cushion, and very probably are the continuation of these same fibres.

Mutilated specimens of forked cells appear to have been seen already by Billroth (fig. 12 of his work, enumerated in the appended bibliography) and Key (fig. 7 *b*, 11 *a*, *d*, *e*). Our description is given chiefly from specimens which were isolated by the aid of extremely fine glass needles, the tissues having either been placed fresh in iodized serum or exposed for some little time to the action of a mixture of pure glycerine with a 0.4 per cent. solution of the bichromate of potassa, in equal parts. By this mechanical method of isolating the cells it is not a rare circumstance for some of the processes to be broken off. The transition from the central processes of the forked cells to the nerve fibres that come out from the nerve-cushion has not yet positively been observed. This is owing, in a great degree, to the fact that the methods employed to display to view the nerves, are of little value in demonstrating and isolating the forked cells, so that a distinct view is almost never obtained of both elements at the same time.

Fig. 302.

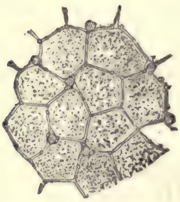

Fig. 302. Surface view of a portion of a taste-disk from the Frog; after a five minutes exposure, when fresh, to the action of iodized serum. The view is taken from above, looking down upon the broad five- or six-angled cup-cells, between which the ends of several cylinder cells and numerous forked cells may be seen in optical transverse section. $\frac{600}{1}$.

In fresh preparations very beautiful optical transverse sections of the prongs of forked cells may sometimes be observed in surface views of the taste-disks. They appear then as extremely small, brilliant circles, lying between the pentagonal and hexagonal cup-cells. Besides these, we can also distinguish the ends of the cylinder-cells as somewhat larger, dull circles, interspersed among the cup-cells.

c. Organs of Taste in Fishes.

The organs of taste in Fishes coincide perfectly, in all material points, with those of Mammals and Frogs. They have been known, since Leydig's discoveries, under the name of *beaker-shaped organs*. They are bud-shaped bodies, composed of peculiar cells and located in the laminated epithelium of the external skin and buccal mucous membrane. From numerous spots in the connective-tissue under layer both of the cutis and also of the mucous membrane cylindrical papillæ, provided with nerves, penetrate into the epithelium; upon the somewhat concave end-surface of each of these papillæ sits a beaker-shaped organ.

Leydig, who discovered these bodies in the external skin of fresh-water Fishes, was inclined to consider them as organs of touch. F. E. Schulze then brought forward strong grounds for interpreting them to be organs of taste. He found them in Fishes in the mucous membrane of the palate, which is supplied with branches from the N. glossopharyngeus; he examined their structure somewhat more minutely and discovered their correspondence, in all essential points, with the organs of taste in the Frog. The entire system of beakers seems, according to Schulze, to be most perfectly developed in the Cyprinoids. Here these organs stand very close to each other in the mucous membrane covering the palate, rudimentary tongue, and inner side of the branchial arches, as well as on the fins; they stand somewhat farther apart in the lips, and farther yet in the skin of the head and throughout the rest of the body. They are wanting altogether in the lips of Cottus gobio and in the external skin of the Pike, Salmon, Torsk, and Herring.

Each beaker-shaped organ consists of a bundle of very long, closely-packed cells which extend from the cutis, or—in the mucous membrane—from

the papilla to the free surface of the epithelium. These cells attain a length of 0.1 mm. or more. In every beaker, according to F. E. Schulze, two different types of cells may be distinguished. The one, corresponding to the cover-cells in the taste-buds of Mammals, and to the cup- and cylinder-cells in the taste-disks of the Frog, occupies chiefly the peripheral portions of the organ. It is composed of long cylindrical cells, blunt at the upper extremity and containing near the centre an elongated nucleus with nucleolus. Below these cells terminate, with frequently a slight diminution in size, in several "thin finger-shaped or jagged processes."

The second variety of cells correspond to the taste-cells of other Vertebrates and are found most abundantly in the central portions of the beaker. They are very thin, long cells, consisting of a small, elongated, ellipsoidal body with two thread-like processes. The body is almost entirely filled with a nucleus containing a distinct nucleolus. The peripheral process is much longer than the central, but, like the latter, it consists of an extremely thin, straight, cylindrical thread. The central process is often (after being subjected to the action of a 0.5—1.0 per cent. solution of the bichromate of potassa) very regularly varicose. The same is sometimes true of the peripheral process.

The connection between these cells and the nerve fibres, that penetrate upwards through the papilla to the base of the taste-beaker, has not yet been observed.

Whether among the numerous apparatuses of sense that are located in the skin of many Invertebrates, and are commonly considered as organs of touch, a few should not be reckoned among the organs of taste, is a question which future investigations will have to determine.

Concerning the *development* of the organs of taste we possess no satisfactory knowledge.*

Methods of Investigation.

In the study of the organs of taste in Mammals, especially where the object of the investigator is, in a short space of time, to familiarize himself with these elements, the lateral organs of taste of the Rabbit and Hare are particularly to be recommended. Both here and in the taste-papillæ the coarser anatomical relations—location, arrangement, number, size, etc.—of the buds can best be learned from sections which have been made from dried preparations and afterwards softened in dilute acetic acid and glycerine. Another way is to harden the preparation for about twenty-four hours in perosmic acid (0.5—1.5 per cent.); the sections obtained from it may then be rendered transparent by placing them in glycerine. The freezing method can also be employed here to advantage. For the study of the minuter structure of the buds and the elements which enter into their composition, maceration in iodized serum (with or without the addition of some chromic acid) is to be recommended. It is also a good plan to leave the specimen for several days in a solution of the bichromate of potassa, varying in strength from 1—2 per cent., to which an equal volume of pure glycerine may very properly be added. Preparations thus treated should then be teased, under a simple microscope, with very finely pointed needles. For this purpose I would recommend most strongly the use of very finely pointed glass rods in the place of the steel needles ordinarily used. Glass points can be obtained of far greater delicacy than those of steel; moreover they are much smoother and adhere less to the tissues. To obtain a view of the ramifications and terminal distribution of the nerves, sections should first be made from dried or frozen preparations and then examined in dilute acetic acid with glycerine. Sections that have been made from

* Later Remark.—In the larvæ of the Frog, F. E. Schulze has recently discovered in the papillæ of the buccal cavity beaker-shaped organs, which in structure corresponded very closely with those of Fishes. Perhaps these are undeveloped specimens of what later will be taste-disks.

fresh preparations—frozen ones are the best—and then treated either with the chloride of gold (0.1—0.5 per cent.) or perosmic acid (0.25—2 per cent.), will be found instructive. To see the distribution of the delicate terminal nerves in the mucous membrane, immediately beneath the taste-buds, Schwalbe recommended especially to macerate the preparation for several days in a solution of chromic acid (0.02 per cent.) or of the bichromate of potassa (0.5—1 per cent.).

The organs of taste in the Frog should first be investigated perfectly fresh in serum. In this way the peculiar epithelium of the taste-disk will be seen in a living condition: it will also be possible to distinguish the nucleated inner from the non-nucleated outer layer, and in surface views to look down upon the mosaic which is composed of the ends of the large cup-cells and the points of the cylinder and forked cells; at the same time the relations of the darkly outlined nerve fibres and the general structure of the papillæ may be included in the observation. The separation of the taste-disks into their elementary parts can best be accomplished by leaving the preparation for several days in a mixture of the bichromate of potassa (0.4 per cent.) and pure glycerine in equal parts, and afterwards teasing it apart with sharply-pointed glass rods, under a simple microscope. An equally good method is to place the preparation for some hours in a solution of perosmic acid, of from 0.5—1.5 per cent. strength. The distribution of the nerves in the nerve-cushion may sometimes be distinctly seen, even in fresh papillæ, provided the taste-disks have first been dissected off in serum. They are then rendered more distinct by the addition of glycerine. Perosmic acid might also be tried in this connection.

To study the cells in the beaker-shaped organs of Fishes, F.E. Schulze recommends *teasing* the preparation, after maceration for a short time in a solution of the bichromate of potassa (0.25—1 per cent.).

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CHAPTER XXXV.

THE ORGAN OF SMELL.

BY PROFESSOR BABUCHIN.

IN the organ of smell we must distinguish three component parts: (*a*), the apparatus which appreciates odors; (*b*), the conducting apparatus; and (*c*), the central organ to which the sensations of smell are transmitted by the conducting apparatus.

The first, and in part also the second apparatus, are embedded in the mucous membrane, which in the higher animals covers the upper and deeper portions of the nasal cavity; in some of the lower Vertebrates (the naked Amphibia) overspreads a species of elevations on either wall of the simply-formed nasal passage; in others (the Fishes) forms numerous but regular folds on the floor of the nasal fossæ, between which or on which are the sensitive elements. We cannot, however, go into a detailed description of all the external peculiarities and modifications of the organ of smell in all the different animals; this belongs rather to the domain of comparative anatomy. Our principal object is to describe the physiological elements of the organ and their relations to each other.

The mucous membrane, which contains the perceptive elements, exhibits peculiarities by which even with the naked eye it can be distinguished from the rest of the nasal mucous membrane. It is either of a yellow color (in Men, Sheep, Calves) or of a brownish color (in Guinea-pigs, Rabbits, Dogs and other Mammalia). For this reason the name of locus luteus has been given to the entire surface covered by this mucous membrane. But, as this portion of the nasal mucous membrane is not characterized by a peculiar color in all animals, it is preferable to adopt another name—regio olfactoria—by which is designated only that region of the nasal mucous membrane where the nerves of smell split up and terminate. There are, however, other characteristics besides the color which mark out this region. The portion of mucous membrane which covers it is thicker, softer, and more succulent than the surrounding portions, and exhibits these peculiarities in different degrees in the different animals. In Birds, for example, this region is resistent, and presents hardly any peculiarities to the naked eye; while, in the Plagiostomata, it looks as if its surface was composed of thick mucus.

The works of Todd-Bowmann,* Eckhardt,† Ecker,‡ and others, have done much for our knowledge of the structure of the olfactory region, but a solid foundation for it dates only from the investigations of Max Schultze.§ Future labors can only concern special details, but not shake the facts discovered by Schultze, as has been attempted by some authors.

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* *Physiological Anatomy*, vol. ii.

† *Beiträge zur Anatomie und Physiologie*, Heft 1. 1855.

‡ "Bericht über die Verhandl. z. Bef. d. Naturwissensch." zu Freiberg, 1855, No. 12, *Zeitschr. für wissensch. Zoologie*, Bd. viii. 1856.

§ *Untersuchungen über die Nasenschleimhaut.* 1862.

An idea of the grosser relations of the olfactory region is best obtained from thin perpendicular sections through the entire thickness of the mucous membrane. These can be most easily obtained, according to my experience, from the mucous membrane after it has been hardened, with the subjacent bone, in a solution of chloride of gold.

Fig. 303.

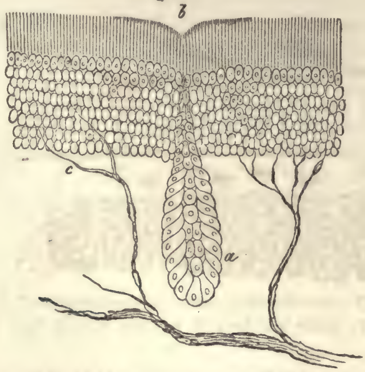

Fig. 303. A vertical section of the septum nasi of the Guinea-pig (chloride of gold preparation). *a*, medulla of the bone; *b*, bone; *c*, periosteum; *d*, glandular layer (not given in detail); *e*, branches of the nerves of smell; *f*, epithelial layer.

In this way the different elements retain their normal position, and are sharply defined from each other. In thin sections of the nasal septum of the Guinea-pig, prepared in this way, we find that the bony portion of the septum is covered with a periosteum, immediately upon which is a thick layer of numerous glands closely packed together (fig. 303). These, "Bowmann's glands," as they are called by Kölliker, are long follicles, which, according to the species of animal, are simple, rather flask-shaped than tubular, or composite with projections and twistings of their blind extremities. For this reason it is seldom possible, in perpendicular sections of the mucous membrane from the higher animals, to follow out a single gland for its entire length, as will be seen in the accompanying wood-cuts; we meet, for the most part, only separate portions at different levels. In the lower animals we can obtain better results. The glands contain an epithelium, which, near their blind extremities, is composed of large, granular, rounded cells, which in some animals contain yellow or brown pigment. Under the influence of the chloride of gold they become of a deep black color. The epithelium has a more polygonal form and is less granular at the outlets of the glands; the outlets extend through the layer above them to the internal surface. Sometimes we find at their mouths a funnel-shaped depression of the mucous membrane. In the lower animals (Frog) it is easy to demonstrate that the entire length of the outlet, up to its termination at the surface of the mucous membrane, is lined with smaller cells. Just back of the mouth we find also small epithelial cells lengthened in the direction of the long axis of the outlet.

At the junction of the olfactory region with the ordinary mucous membrane the glands become less numerous, and finally disappear, giying place to the ordinary mucous glands.

According to Kölliker, in Man, even in the olfactory region, we find ordinary mucous glands instead of those which have just been described,

but M. Schultze asserts that these glands represent a transition form and remind one of the Meibomian glands.*

Fig. 304.

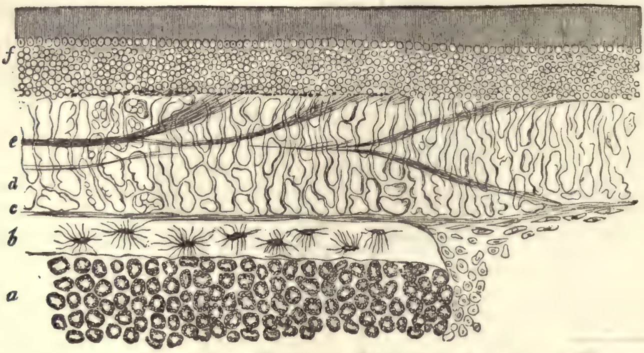

Fig. 304. Section of the olfactory mucous membrane of the Frog. *a*, Bowmann's gland; *b*, its outlet; *c*, little bundles of nerves which run between the epithelial cells.

In Fishes the glands are entirely absent and are replaced by mucous cells. Between the glands we find ordinary connective tissue, which near the bones becomes continuous with the periosteum, and externally borders on the epithelial layer. I have been unable to find here a special basement membrane, such as Hoffmann describes. This membrane is only the appearance produced by the line of demarcation between the connective tissue and the epithelium. In both the superficial and deep layers of the connective tissue there are many fusiform and branching cells, which, especially in the lower animals, may contain black pigment. M. Schultze has also observed in the higher animals pigment cells and free masses of pigment. We also find embedded in the connective tissue vessels and branches of the olfactory nerves, which are particularly plain in chloride of gold preparations.

The outer layer of the olfactory mucous membrane consists of epithelium. In gold preparations, as is represented in fig. 303, we can distinguish two portions in this layer: an outer finely striated and an inner granular layer. Eckhardt and Ecker have in part described the real condition, but the fine researches of M. Schultze have completely demonstrated the structure of this epithelial layer. By these researches it is shown, that in all Vertebrates the epithelial portion of the olfactory organ is formed after one and the same type, so that a description of the structure of this part in any one animal is sufficient to give a complete and correct representation of it in all. We therefore choose an animal in which the epithelial cells are large and easily isolated, as in the Proteus, in which the physiological elements reach a gigantic size, and have as yet been but little examined. If we first place the entire olfactory organ of a Proteus in Müller's fluid for a day, then leave it for a day in distilled water, and finally pick apart a portion of the olfactory region, it can be plainly seen how the epithelial layer is composed of separate groups of cells. Of these groups we distinguish an outer half, apparently composed of the finest threads, which is furnished at its outer

* M. Schultze has since this observed racemose mucous glands in the olfactory region of Man. *Centralbl. für med. Wissensch.* 1864. No. 25.

end with long cilia, and an inner, composed of large, closely packed nuclei, of which one is larger than the rest, is of oval form and is usually placed externally. A further isolation of the elements shows that each of these groups is composed of two kinds of cells : a few large, and numerous other cells, each of which has a large, round nucleus, and very long, fine processes (fig. 306). The largest of these processes runs outwards; the other is very fine, runs inwards, and can be followed up to the edge of the sub-epithelial connective tissue. These are the olfactory cells of M. Schultze, which have the property of perceiving odors. Their outer ends bear the long, fine cilia * already mentioned, and appear in preparations macerated in Müller's fluid, of zigzag and undulating shape. In gold preparations, or in those treated with sulphuric acid, these processes appear as fine, varicose threads.

Fig. 305.

Fig. 306.

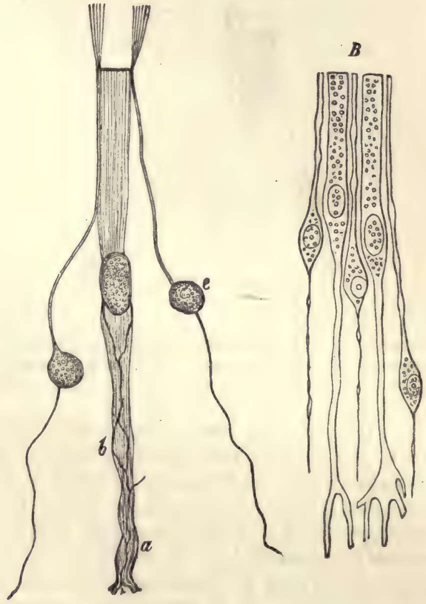

Fig. 305. A group of olfactory cells from a Proteus, with some of the inner epithelial cells (Müller's fluid). *a*, an isolated olfactory cell, after maceration with very dilute sulphuric acid.

Fig. 306. *A*, *a*, epithelial cells from the olfactory region of a Proteus (Müller's fluid) ; *b*, the apparent processes ; *c*, olfactory cells ; *B*, epithelial and olfactory cells from Man, after M. Schultze.

With stronger magnifying powers it can be demonstrated that a fine continuous thread may be traced through all the varicosities. From this we may conclude that the outer process of the olfactory cell consists of two substances throughout its entire length : an outer, which swells up under

* This apparent contradiction on the part of Max Schultze, according to whom the cilia in Proteus are wanting and must, as in those animals that breathe by means of gills, necessarily be wanting, can only be accounted for by the fact that this profound observer only had a single animal at his disposal—one that had been preserved for a long time in a solution of bichromate of potassa.

the influence of certain reagents, and an inner thread, which remains unaltered. The central process of the olfactory cells shows the same conditions, with the difference that it is much finer, and often has a thickness which can hardly be measured. I have found in Tritons that the length of these processes with that of the other portions of the olfactory cell is sometimes much longer than the thickness of the epithelial layer (fig. 307). They must, therefore, either penetrate into the sub-epithelial layer, or run in a horizontal direction along the edge of the epithelial layer. The second condition I have actually observed in the Proteus. The cells just described surround on all sides the large cells mentioned above, which have a large oval nucleus and penetrate through the entire thickness of the epithelial layer; their outer halves appear more or less cylindrical, in the Triton and Proteus are transparent, and often plainly striated in their long axes

Fig. 307.

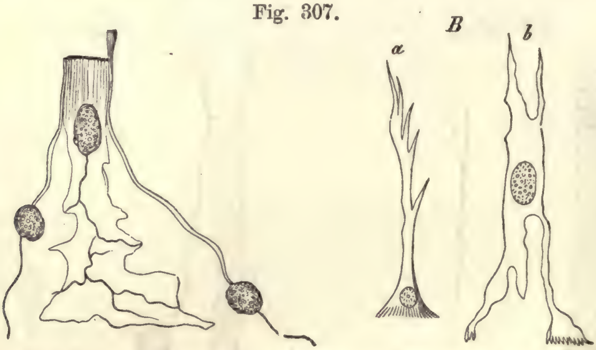

Fig. 307. *A*, an epithelial and two olfactory cells, from the junction of the olfactory and ordinary mucous membrane (Triton); *B*, peculiar epithelial cells from the olfactory mucous membrane; *a*, the Raja elevata, after M. Schultze; *b*, the Proteus.

(fig. 306). I have been able to convince myself that this striation is not due to the surrounding olfactory cells. The striation does not involve the entire thickness of the cells, but only their surfaces. At the outer ends of the cells, which are free from cilia, we can distinguish a series of small points, which surround the entire end, but do not resemble the edge of an ordinary cylindrical epithelial cell. The inner half of these cells is not so regularly formed as the outer; but I doubt the assertions of some authors, that it is composed of branching processes. Its form is very variable, and we can consider it as if this half at first had the appearance of a thick or thin cylinder, composed of a soft, transparent substance, into which the round bodies and the nuclei of the olfactory cells were pressed from all sides. In this way folds are formed of which the edges appear sharper than the surrounding substance, and in their course form figures, and simulate the processes spoken of by other authors. But we can demonstrate with aniline staining that a very fine, transparent substance is stretched between these processes, which has longitudinal striations. The independent nature of this striation is here still more evident, for the reason that here there are no impressions produced by any thread-shaped elements. The inner process swells into a cone close to the subjacent connective tissue, and then splits up into numerous short threads. It is very remarkable that, under the influence of some reagents, the inner process has a different appearance. If epithelial cells from the Proteus, which have been treated with Müller's fluid, or iodized serum, are soaked for some time in dilute

glycerine, the transparent substance disappears, and the folds mentioned above look like branching processes. If we treat with nitrate of potash the mucous membrane of the olfactory region in animals in which this is but slightly pigmented, we retain a very elegant picture, which shows at once how the olfactory cells are situated relatively to those just described. We bring into view figures which represent the ends of the large cells surrounded by a great number of black points, which according to the species of animal are more or less thickly packed, and are really the ends of the olfactory cells (fig. 308).

The relations just described are repeated in all animals, including the Invertebrates (Cephalopods, Sernoff), with trifling modifications. Thus, for example, M. Schultze has asserted that in Mammalia, and also in Man, the olfactory cells possess no cilia, or as he calls them olfactory hairs, which only means that these hairs do not represent a necessary condition in the perception of smell and are not therefore deserving of any special name. Where the olfactory hairs exist (Birds, Amphibia) they appear as stiff hairs, of which only one of great length is attached to each olfactory cell, or as bundles of fine cilia. These again are motionless or have a slight motion of their own. In some animals there are olfactory cells with both kinds of hairs. Sometimes that portion of the olfactory cell which contains the nucleus has a fusiform shape. In some animals the outer processes are much thicker, in others more delicate, and become varicose after maceration in fluids. M. Schultze has also shown that the large epithelial cells in some Mammalia are more or less pigmented, and that the yellow pigment is situated either in the outer or inner portion of these cells, by which the color of the olfactory region already mentioned is in part produced. In the Mammalia and in Man there are only epithelial cells without cilia in the regio olfactoria proper, and although near these there are in places ordinary ciliated epithelial cells, yet between these last there are no olfactory cells. In the Plagiostomata, on the contrary, the olfactory region is principally covered with ciliated epithelium.

Fig. 308.

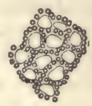

Fig. 308. The surface of the epithelial layer of the olfactory region treated with nitrate of silver. (Proteus.)

Besides the two kinds of cells described, there is in the Plagiostomata (M. Schultze), in the Proteus and Triton (myself), and perhaps in many other animals, still another species of cell situated in the epithelial layer, which resembles Engelmann's fork-shaped cells. Their form is very variable and may be seen in the accompanying figures (fig. 306, *B*). Their central end rests on the subepithelial layer and breaks up at that point into fine threads. Their peripheric end does not reach to the surface of the epithelial layer, and either terminates in a conical point or is branched. Their form is, as already mentioned, very variable. Thus we find in the Proteus cells which, from their branching form, resemble multipolar nerve cells.

Finally we often find, especially in young animals, in the deeper portions of the epithelial layer round cells without any processes, which must be considered as material for the formation of the olfactory and epithelial cells.

The conducting apparatus of the organ of smell consists of the olfactory nerves, which arise from the bulbus olfactorius by one or by several trunks, according to the species of animal, and are then distributed in the mucous membrane of the olfactory organ. The nerves, which can be easily split into bundles, run in an oblique or horizontal direction in the glandular

layer. From these trunks numerous branches are given off which bifurcate repeatedly at various angles and run outwards into the epithelial layer. In gold preparations they can be traced up to the surface of this layer. In the opposite direction the nerves run to the bottom of Bowmann's glands.

As to the finer structure of these nerves, this has already been sufficiently examined by M. Schultze and is described on pages 121 and 122 of this book. I cannot, however, agree with this observer, that the olfactory nerves contain primitive nerve fibres, which are formed after the type of the fibres of Remak, that is, of a nucleated sheath of Schwann and fibrillated contents. According to M. Schultze's representation, the olfactory nerves break up into bundles of primitive fibres. In some animals these bundles consist of fibrillæ, and are contained in a nucleated sheath, which he calls the sheath of Schwann. In other animals, again, the bundle of primitive fibres breaks up within its sheath into primitive fibres, of which each one consists of fibrillæ and of a sheath of Schwann. According to my experience in all animals the bundles in question, whether they have or have not sheaths, are composed of the finest fibrillæ, held together by finely granular matter. In some animals, besides this, nuclei may be arranged between the fibrillæ in regular rows, so that the entire bundle is separated into secondary bundles without sheaths. The sheath of the primitive bundle cannot represent the sheath of Schwann; it is rather to be compared with the neurilemma from a morphological point of view, whatever its properties and structure may be. We must also assume this where there are no nuclei between the fibrillæ, and no secondary bundles are formed, as is the case, for example, according to M. Schultze, in the Pike. If we should consider the sheath in this case as the sheath of Schwann, we must also do so where the fibrillæ split up within the sheath into secondary bundles, which according to M. Schultze are also provided with sheaths of Schwann; this would signify, in other words, that nerve fibres invested with sheaths of Schwann were enclosed together in a common sheath of Schwann. I may add also that in many animals, especially in the Plagiostomata, I have not been able to convince myself that the primitive bundles of fibres contained any such sheaths. The method of development of the peripheric nervous system makes it probable that the olfactory nerves should be considered as embryonic nerves, which have been arrested at the second step of their development, while the fibres of Remak reach a farther point in their development. The nuclei which are found between the fibrillæ of the olfactory nerves are, for the most part, veritable cells. They have frequently a fusiform shape, and their fine processes adhere closely to the nerve fibrillæ. I shall have an opportunity to speak still more fully of this subject at another place in this book.

The question now presents itself, what becomes of the nerve fibrillæ after they have reached the epithelial layer? We can only answer this question hypothetically. Attempts made with the gold-staining have not demonstrated that the nerve fibrillæ terminate as they do in the cornea, which is what we would naturally expect. After having found that the large epithelial cells are undoubtedly covered with fine longitudinal striæ over their entire length, although these striæ can only be seen under favorable conditions, we might suppose that the finest fibrillæ of the olfactory nerves, after they had passed through the epithelial layer, surrounded the large epithelial cells on all sides and with them reached to the surface of the epithelial layer. This supposition could be strengthened by the fact that the cone-shaped inner ends of the large epithelial cells break up into fine fibres. But I think that for the present such a supposition would be rather too

sanguine. The number of observations published concerning striated cells increases every day. Thus, for example, it has been long known that the lens fibres often appear striated in their long axes. Pflüger has observed striation of nearly all the cells which make up the salivary glands. I have myself seen that a regular striation is formed on the crystalline body of some Sea-crabs under the influence of certain reagents. Finally, I have observed that the contents of the beaker cells sometimes look as if they were composed of fine fibres. This warns us to be careful in explaining the striæ and not to consider everything to be nervous that is striated. I must also call attention to the fact that in the Triton, at the junction of the epithelium of the olfactory region with the ordinary epithelium, where the olfactory and epithelial cells become thicker and shorter, the inner ends of the epithelial cells are very broad and show no striation (fig. 306).

M. Schultze has already for some time past spoken of the hypothesis that the fibrillæ of the olfactory nerve are continuous with the inner ends of the olfactory cells. As the principal support of this hypothesis he calls attention to the complete chemical and morphological analogy between the central ends of these cells and the nerve fibrillæ. As a farther proof of this hypothesis, I may add that the olfactory nerves are stained of a blackish-violet color by the chloride of gold, and that occasionally the processes of the olfactory cells are stained of the same color, while their nuclei remain white and transparent. I possess a preparation from a Tortoise, one out of many hundred sections, in which can be observed the immediate passage of the nerve fibrillæ into the epithelial layer. From the deeper branches of the olfactory nerve the twigs pass almost perpendicularly into the epithelial layer. These twigs are fibrillated and possess nuclei. After still farther subdivision they reach the edge, and there break up into a few fibrillæ and very fine bundles, which spread out horizontally and like a fan for a short distance, and then run in a perpendicular but tortuous course into the epithelial layer, where they can be followed up to the nuclei of the olfactory cells. This might well raise M. Schultze's hypothesis to an actual fact, if we possessed in the chloride of gold a substance which only stained the nervous elements, and if this reagent were not so very uncertain in its action. There is also, as was mentioned above, in the epithelial layer of the olfactory region a particular kind of cells—very similar to Engelmann's forked cells. It is a matter of taste whether or no to consider these as the terminations of the nerves.

We can often obtain pictures, in which it is evident how the nerve fibrillæ joined in bundles penetrate into the epithelial layer and pass far outwards between the epithelial cells, which would lead to the supposition that they terminated by free extremities (fig. 304, *c*.) This contradicts apparently what has been previously said concerning the termination of the nerves, but only apparently. When we remember that, as I have convinced myself after observing every precaution, the olfactory region is also sensitive; when we farther remember how probable it is that sensation and smell are effected by different nerves, it becomes very natural to consider the free termination of nerves observed by me as belonging to the sensitive fibres. M. Schultze has in addition observed medullated fibres between the non-medullated. Not less difficult to answer is the question of the relations of the olfactory fibrillæ to the central portions of the organ of smell. It has been known for a long time through the works of Walter,* Leydig,† and M. Schultze,‡ and has

* Virchow's *Archiv*, xxii. † *Lehrbuch der Histologie*, 1857.
‡ Loc. cit.

been recently confirmed by Meynert,* that the olfactory fibrillæ arise in bundles from large globular bodies, which are embedded in the bulbus olfactorius. Yet, as Kölliker says in his book, it has not yet been possible thoroughly to establish the finer structure of these bodies. The best results are to be obtained by examining the various relations of these bodies in the Plagiostomata, in whom the same constituent parts which make up the central apparatus of the higher animals are separated from each other and independent. In the Torpedo, for example, the bulbus olfactorius is situated immediately at the olfactory fossa and is joined by the long and slender tractus olfactorius to the anterior temporal lobes. The membrane covering the tractus is continuous with that covering the bulb, in which the rounded bodies mentioned above are irregularly scattered.

They are separated from each other by nerve fibres and vessels, possess a finely granular structure, and appear to be covered with nuclei. In the Torpedo it is easy to demonstrate that these apparent nuclei are really small nerve cells; some of which are bipolar, the majority multipolar. One of the processes of these cells sometimes appears smooth and runs towards the olfactory tract, where it becomes covered with medulla. The other processes are at first thick, then break up into a number of branches, which pass into the globular bodies. If a nerve cell is bipolar, the finer process passes into the olfactory tract; the other process, which is distinctly fibrillated, passes into the rounded bodies, where it breaks up into fine fibrillæ. The fibrillæ are sometimes spread into a sphere without any order and pass out from one side of it united in bundles; sometimes they are united into a bundle in the sphere, run a tortuous course, and are joined to the other bundles of the olfactory nerves (fig. 309).

Fig. 309.

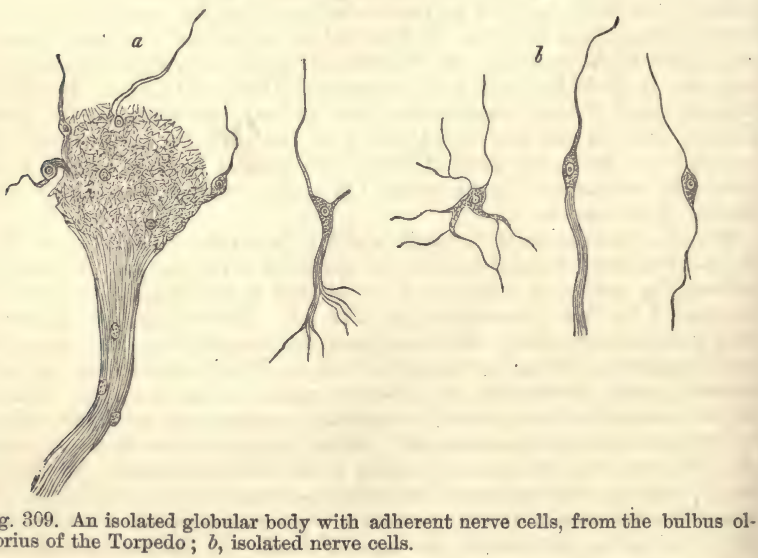

Fig. 309. An isolated globular body with adherent nerve cells, from the bulbus olfactorius of the Torpedo; *b*, isolated nerve cells.

What can be the morphological signification of these spherical bodies? Are they peculiar formations, or do they have analogies in the nervous system?

* *Vierteljahrschrift für Psychiatrie*, ii. Jahrg., 1, 4, 102.

Although at the first glance they appear finely granular, yet in very thin sections they appear to have the same structure as the so-called molecular layer of the retina. But I do not think it would be entirely correct to assume that we have here a reticulated or spongy connective tissue. It is rather a coil of the finest fibrillæ, of which we know the origin, and between which there is an abundant finely granular mass. We find the same relations in every place where there are only nerve fibrillæ, or, in other words, where the axis cylinders are bare, or where the nerves have not reached the higher degrees of development. If such fibrillæ run parallel to each other, as is the case with the embryonic or the olfactory nerves, then the bundles of fibrillæ have a striated, granular appearance. The finest granules, or perhaps a substance which is changed into granules by certain reagents, stick so fast to the fibrillæ and glue them so closely together that it is difficult to isolate them.

If the fibrillæ have an irregular and complicated course, then we have the appearance of reticulated connective tissue, which is principally produced by the granules; then it is nearly impossible to isolate the nerve fibrillæ, as is the case with the globular bodies of the regio olfactoria. I am very much disposed to assume that the same relations are repeated in the retina and perhaps in other portions of the nervous system.

The tractus olfactorius consists exclusively of medullated nerve fibres, which have no sheath of Schwann. After they have reached one of the two projections, which in the Torpedo are situated on both sides of the large hemispheres, they penetrate into the reticular substance, gradually lose their medullary covering, and are joined with numerous small nerve cells, of which some are bipolar, the others multipolar. This constitutes the only certainty which I have found from my examinations of the central apparatus of the organ of smell in the Plagiostomata. Any further elements of this apparatus were inaccessible to me, and the literature gives no sure account of them. All the relations, however, which have been described of the origin of the nervus olfactorius are also true for the higher animals—no matter how different the structure may appear at the first glance. In every case the fibres of the tractus olfactorius spring immediately from a finely granular, reticulated mass, whether they have the form of globular bodies or some other.

This mass is in all cases covered with small nerve cells. The processes which run inwards to the olfactorius and the cerebrum are in all cases changed into medullated nerve fibres, which are again united with other nerve cells. The only difference, therefore, is in the topography of the parts, and is merely accidental. This belongs to another chapter of this book.

During the last revision of these sheets Exner (*Wiener Sitzungsberichte*) has published some observations on the olfactory mucous membrane of the Frog. According to what I can gather from his paper, the branches of the olfactory nerve break up into a meshwork between the connective tissue of the mucous membrane and the epithelium, from which arise the central processes of the olfactory cells and of the epithelial cells. The fibres of the trigeminus form a plexus with wide meshes in the connective tissue of the mucous membrane.

CHAPTER XXXVI.

THE ORGAN OF VISION.

1. The Retina.

By MAX SCHULTZE.

The retina is the membranous terminal expansion of the optic nerve in the background of the eyeball. It contains, besides nerve fibres, various forms of nerve cells, which are distributed in the course of the fibres before they reach their peripheric extremities; these extremities being distinguished by a peculiar terminal apparatus, namely, the rods and cones of the retina, which are surrounded by pigmented sheaths. The nerve fibres and nerve cells of the retina are embedded in a spongy connective substance which may be considered as a continuation of that of the optic nerve, and which is very similar to the connective substance of the central organs of the nervous system. Blood-vessels and perhaps also lymphatic vessels make up a part of this connective substance.

The elements of the retina arrange themselves in layers parallel to the surface of the hollow sphere formed by the coatings of the eyeball. The innermost of the retinal layers, lying next the corpus vitreum, is the membrana limitans interna. Its attachment to the vitreous, especially in the region of the ora serrata, under some circumstances renders the separation of the retina exceedingly difficult, whether in the fresh or in the well-preserved state. The outermost of the layers is that of the rods and cones, including the pigment sheaths, which are formed by a special cell-layer, namely, the pigmented cell-layer of the retina. This layer lies upon the choroid, and in fact upon the transparent connective substance of the choriocapillaris, and often remains attached to the same when the retina has been removed, in which case the rods and cones, being withdrawn from their pigmented sheaths, constitute the outermost layer of the retina. On the other hand, portions of the rods and cones often remain behind with the pigment on the choroid, since in well-preserved specimens the pigment-layer does not readily let go of that portion of the rods which it encloses : thus the outer segments of the rods remain attached to the choroid, while the inner segments go with the retina.

The divisions of the retina are manifold, and the synonyms in the nomenclature threaten to render difficult the understanding of ophthalmological literature. It is therefore important to unite upon the simplest possible method of designating the various layers. The names which Heinrich Müller consistently employed in all his publications on the retina have remained the most current, and may be retained with some modifications. Only the membrana limitans externa (M. Schultze) is newly introduced, and H. Müller's intergranular layer is divided into two distinct layers. I first called attention to the necessity of this division, and left the name of intergranular layer to the constant stratum of fine granular appearing substance which lies between the inner and outer granules, but separated

from it that modification of the layer of outer granules (considered by H. Müller to be a part of the intergranular layer*), which is highly developed in the macula lutea of Man, and which consists of rod- and cone-fibres. Henle names the intergranular layer (as I define it) external molecular (äussere granulirte) layer, and thus expresses its similarity in structure with the molecular (innere granulirte) layer, but applies the name external fibrous layer to the fibrous, radiating, inner division of the external granule-layer. To avoid mistake in the apprehension of the name intergranular layer, which as shown above means something different in H. Müller's publications and in mine, Henle's designation, external molecular layer, will be used in the following treatise instead of "intergranular layer." The following summary, therefore, gives the nomenclature of the retinal layers as here employed, enumerating from within outwards:—

1. Membrana limitans interna.
2. Layer of optic-nerve fibres.
3. Layer of ganglion-cells.
4. Internal molecular layer.
5. Layer of internal granules.
6. External molecular (intergranular) layer.
7. Layer of external granules, including the external fibrous layer which exists in certain portions of the retina.
8. Membrana limitans externa.
9. Layer of rods and cones.
10. Pigment layer.

All these layers of the retina, which lie between the two boundary layers, are made up of the two different elementary parts already mentioned, namely, elements of nerve tissue and elements of connective substance. This much is undeniable. On the other hand, the greatest diversity of opinion prevails on the question to which of the two groups of tissues this or that fibre, this or that cell, should in a particular case be reckoned. This depends upon the fact that our researches concerning both the peripheric and centric extremities of nerves everywhere meet with the unsurmountable obstacle that very fine non-medullated nerve fibres cannot be distinguished by any perfectly sure characteristic from fibres of another nature, not even by high magnifying powers; especially is this so when both kinds of fibres are intimately interwoven, as is doubtless the case in many portions of the retina. In order to obtain a foothold for the distinction of these two kinds of fibres, we shall start in the study of the finer structure of the retina with the unmistakable nerve fibres, as they diverge from the optic nerve and form the layer of optic-nerve fibres lying next the membrana limitans externa. With the results here obtained we shall learn to search out and distinguish the nerve fibres also in other layers, in which the continuous communication of the nervous elements can no longer be proven. The supporting connective tissue we shall afterwards describe in a special section, as well as the variations which the structure of the retina undergoes at the macula lutea, the fovea centralis, and the ora serrata. The vessels of the retina have their description in another place.

1. The Nervous Elements of the Retina.

The optic nerve, at the point where it reaches the external surface of the eyeball, as well as in its entire course through the orbit, consists, with the

* Compare H. Muller, *Z. f. w. Z.*, Bd. viii., Taf. ii., Fig. 17, 3.

exception of its sheath, its blood- and lymph-vessels, of medullated nerve fibres, which are grouped in bundles and embedded in a rather firm connective tissue. By tearing up small fragments in the fresh state and examining them in indifferent fluids there will be brought to view only short pieces of nerve fibre with drop-like masses of nerve medulla, elements which resemble those of the white substance of the brain.* Longer pieces of medullated

Fig. 310.

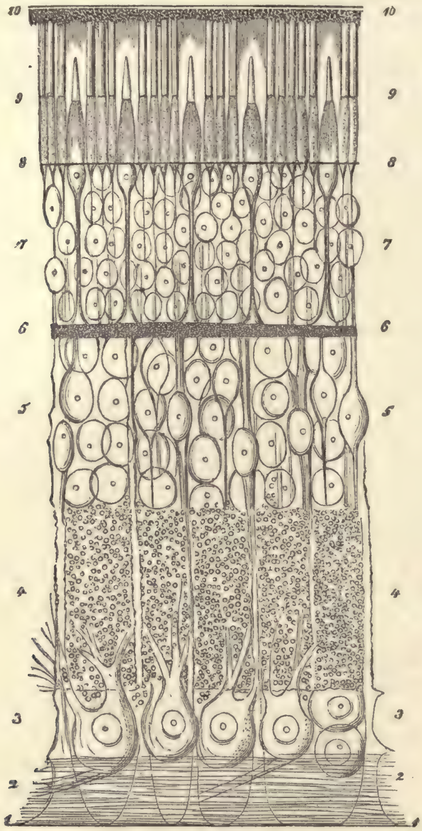

Fig. 310. View of the layers in the Human retina. ×400. The numbers refer to the above summary in the text.

nerve fibres may be isolated by tearing up fine longitudinal sections of an optic nerve which has been previously hardened in preservative fluids. These also, with the enlargements and varicosities which they present, are like the similarly treated medullated nerve fibres of the white substance of the brain.† We must therefore assume that the fibres of the optic nerve,

* Ehrenberg first described and illustrated by many drawings this similarity of the optic-nerve fibres with the fibres of the brain, and the dissimilarity of other peripheral nerves. *Abhandl. der Acad. der Wissensch. zu Berlin*, 1854, p. 665. Taf. i.–v.

† Comp. this text-book, p. 119, fig. 31.

like those of the brain, are destitute of the sheath of Schwann. If, on the other hand, the consistence of the substance of the optic nerve is altogether greater than that of the brain substance, this is sufficiently explained by the great quantity of firm connective substance which is contained in the optic nerve, and of the existence of which one may convince himself on observing thin sections of hardened nerve.

Each bundle of nerve fibres is separated from its neighbor by a thick layer of fibrous connective tissue rich in blood-vessels,* so that on careful estimation the bundles of nerve fibres scarcely make up half the volume of the optic nerve. In each bundle are mingled nerve fibres of very different thickness, the finer fibres exceeding in numbers. As the optic nerve perforates the sclerotic at the so-called lamina cribrosa, all the nerve fibres lose their medullary sheaths, with the exception of certain cases hereafter to be mentioned. The consequent diminution in thickness of the optic nerve is quite abrupt, and is also occasioned, according to Löwig,† by a continuity of the inner connective substance of the nerve with that of the sclerotic and choroid. There now remains of the nerve fibres the exceedingly delicate axis cylinders, apparently destitute of medullary sheaths. These axis cylinders surrounding the central artery and vein, and still enveloped in a certain amount of connective substance, pass through the choroid, lining the shallow crater of the optic-nerve excavation,‡ and radiate in all directions in the plane of the inner surface of the retina; thus forming the layer of optic nerve fibres which lies just external to the membrana limitans interna, and whose thickness gradually decreases in approaching the ora serrata, so that at that point only isolated fibres or bundles of fibres are to be seen. At the yellow spot of the retina the nerve fibres as a continuous layer suffer an interruption. The remains of the connective substance of the opticus are continuous with the supporting fibres of the retina. §

The nature of this layer consisting of nerve fibres may be studied in the perfectly fresh state by placing under the microscope, with the internal surface upward and moistened with vitreous fluid, pieces of retina from the still warm eyeball. The most distinct pictures may be obtained in the vicinity of the ora serrata, where the nerve fibres are isolated and the entire retina is thinner and more transparent, provided that the granular coagulation, which attacks most of the cellular elements of the retina soon after death, has not yet taken place. The isolation of the delicate fibres by tearing them up in the fresh state and in indifferent fluids can be only very incompletely accomplished; it may, however, succeed with properly hardened

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* Compare the descriptions and drawings of transverse and longitudinal sections by Donders in Graefe's *Archives*, Bd. i., Abth. 2, Taf. ii., figs. 2 and 3; by Henle, *Eingeweidelehre*, p. 583; and by Leber, Graefe's *Archives*, Bd. xiv. 2, Taf. v., fig. 1. Such sections present exceedingly instructive pictures, if taken from optic nerves which have been hardened by immersion for a short time in a strong solution of osmic acid, or, according to F. E. Schultze, in chloride of palladium, or, if the sections taken from nerves previously hardened are colored with chloride of gold (Leber), and show, as Klebs (Virchow's *Archiv*, Bd. xix., p. 324) declared, that the amount of connective tissue in the optic nerve is often much more considerable than appears in fig. 3, Tab. xix. of the *Icones physiologicæ*. The difference between the normal and atrophic optic nerve is described very accurately by Leber.

† *Studien des phys. Inst.*, Breslau, edited by Reichert. 1858, p. 125.

‡ H. Müller, in Graefe's *Archiv f. Ophthal.*, Bd. iii., Abth. 2, p. 86, treats of the so-called physiological excavation of the optic-nerve entrance. Also details of the recent literature are given by L. Mauthner, *Lehrbuch der Ophthalmoscopie*, 1868, p. 252.

§ Klebs, in Virchow's *Archiv*, Bd. xix., p. 321, Taf. vii.

and macerated retinæ, for example after longer or shorter preservation in iodized serum, weak solutions of chromic acid and bichromate of potash. The nerve fibres of the retina thus brought to view are of various size, many being almost too fine to measure, that is to say, less than ½ μ in thickness, the largest measuring 3–5 μ. None show a single trace of nucleus lying upon or within the substance of the fibre; likewise there is no appearance of a separable sheath or a division into cortex and medulla. They are pale, flexible, very soft fibres, in which no other structure can be observed than the indication of a delicate striation and here and there a collection of fine granules. All display a great tendency to the formation of spindle-shaped varicosities. In fresh preparations in situ these varicosities are almost entirely wanting: their formation can be hindered by the use of iodized serum with the addition of common salt, and is promoted by diluting the serum with water; this is therefore a peculiar appearance due to swelling.

The number, the size, and the form of the varicosities are manifold, but their appearance is always quite different from that of the medullated fibres of the brain or spinal cord. In the case of the latter the nodular, varicose contour is caused by a partial projection of the highly refractive nerve medulla, of which there is here no vestige. These spindle-shaped varicosities of the optic-nerve fibres resemble rather the appearances presented by axis cylinders which have been isolated from their medullary sheaths, as for instance in fibres of the acoustic nerve.*

The circumstance that the varicosities, especially of the larger fibres, exhibit a granular transformation of the fibre-substance, while the unswollen places remain unchanged and permit the fibrillated structure to be seen more or less plainly, proves that a change in the texture of the nerve fibres has taken place at those points where the varicosities exist.

Fig. 311.

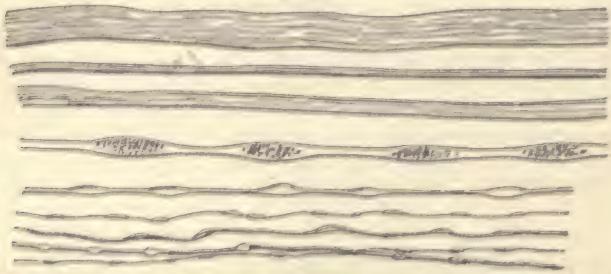

Fig. 311. Nerve fibres of the retina with and without varicosities; *a*, from the Ox, the others from Man. × 800.

The behavior of the nerve fibres of the retina when treated with solutions of chromic acid also proves that these appearances are largely due to swelling by imbibition, since the more concentrated solutions hinder the formation of varicosities, while the weaker the solution the greater their number and size, until the fibres, thick with beadlike swellings, succumb to longer maceration.† This happens first to the finest fibres, whose varicosities are

* M. Schultze, *Observationes de retinæ structura penitiori*, 1859, fig. 1.

† More specific mention of the solutions which cause varicosities in the optic-nerve fibres of the retina may be found in my treatise in the *Monatsberichten der Academie der Wissenschaft zu Berlin*, 1856, p. 511.

from the beginning relatively more numerous and more extensive than those of the largest fibres.

Bifurcations of the nerve fibres have been described and drawn by Corti * and Gerlach.† They occur very seldom, if at all, in the optic-nerve fibre layer. The cases mentioned refer possibly to processes of ganglion cells.

The regular radiating course of the nerve fibres in the retina is interrupted at the yellow spot, according to Michaelis, H. Müller, Henle, Kölliker and others, in so far that here a continuous fibre layer is wanting, the nerve fibres hiding themselves rather in the thick ganglion-cell layer, and in the neighborhood of the yellow spot assuming a curved course, so as to be able to approach it in sufficient numbers. Liebreich‡ recently called attention to another variation, which consists in the fact that many more nerve fibres pass from the optic-nerve entrance perpendicularly upwards or downwards than outwards, in which latter direction, however, a much more extensive retinal surface is to be supplied. The fibres then pass, in company with the larger vessels, around the macula lutea to the external portions of the retina, there to end.

By microscopic examination of the inner surface of an uninjured retina, one may often see a grouping of the nerve fibres in bundles, between which long, spindle-shaped interstices remain.§ At these points groups of the radial supporting fibres push themselves between the bundles in order to end in the membrana limitans interna. At the places where the nerve fibres are very scarce, as at the ora serrata, or where they are wanting as a continuous layer, as at the macula lutea, the ganglion cells lie immediately against the limitans interna.

In exceptional cases the nerve medulla of the optic-nerve fibres of Man persists, even after passing into the retina. From this cause the corresponding portions of a retina are untransparent, and appear white by reflected light, as is portrayed in the excellent ophthalmoscopic plates of Liebreich, *Atlas der Ophthalmoscopie*, Taf. xii., figs. 1 and 2. Since Virchow ‖ noticed the first such case in the cadaver (a man forty-six years of age, both whose eyes exhibited medullated fibres around the nerve entrance, one in the form of four diverging pencils, the other in the form of a dusky white ring), a series of similar cases have been observed, both in the course of anatomical and ophthalmoscopic studies. These cases differ in arrangement, for in some the portions of retina containing the medullated fibres communicate directly with the optic-nerve entrance,¶ in others isolated white spots, remote from the papilla, betray a layer of medullated fibres, so that here the medulla, having disappeared at the nerve entrance, reappears after a certain distance in the course of the nerve fibres.**

Among the Mammalia such a continuation of the medullated nerve fibres into the retina (Bowman) occurs normally in the Rabbit †† and Hare. In these animals there exist two white bundles radiating in opposite directions from the nerve entrance, rendering the retina quite opaque, but, probably, not entirely preventing the perception of light, since the layer of rods, as I have convinced myself, is well developed behind. A small quantity of medullary substance, which, however, scarcely interferes with the transparency of the nerve-fibre layer, is found about the retinal nerve fibres of many Fish, as was remarked by Leydig, who says with regard to the prim-

* Müller's *Archiv*, 1850, Taf. vi., fig. 3.

† *Handbuch der Gewebelehre*, 1854, p. 498.

‡ Zehender, *Klinische Monatsblätter f. Augenheilkunde*, Jahrg. vii., 1869, p. 457.

§ Compare H. Müller and Kölliker, *Retinatafel in Ecker Icones*, etc., fig. 14.

‖ His, *Archiv*, Bd. x., p. 190.

¶ Dönitz (Reichert and Du Bois-Reymond, *Archiv*, 1864, p. 741), in whose eyes this appearance was observed ophthalmoscopically, noticed that the affected portion of the retina, like the optic-nerve entrance, was blind; in other words, either the retina was opaque, or the rods and cones were wanting behind.

** For instance, in Recklinghausen's case, Virchow's *Archiv*, Bd. xxx., p. 375.

†† Compare H. Müller's *Z. f. w. Z.*, Bd. viii., p. 64, Anm.

itive nerve fibres of the Roach and Dog-Fish, "they have sharp contours and are varicose."*

H. Müller also mentions that a portion of the fibres within the eyeball of Fishes is composed of axis cylinder and medullary sheath.† Something similar is seen likewise in Birds.

A remarkable variation from the normal condition is displayed in the thickening of the nerve fibres of the retina, first recognized as cause of the white spots occurring in the retina in cases of Morbus Brightii, and considered as bipolar ganglion cells. These bipolar ganglion cells, which were first described by Zenker and Virchow, and whose true nature was first perceived by H. Müller,‡ present similar varicosities, spindle-shaped thickenings and condensations of the non-medullated fibres, whose substance in these cases is firmer and more brilliant and resists decomposition longer than the normal axis cylinder.

Division of the nervus opticus within the orbit is followed by atrophy of the nerve-fibre layer (Lehmann), which, according to Krause, is preceded by a deposit of molecular fat in the transparent pale fibres, and this fatty degeneration also spreads to the next layer, namely, the layer of ganglion cells.

Externally to the nerve-fibre layer lies, spread out over the greater portion of the retina, and separated by larger or smaller intervals, a single layer of nerve cells or nerve bodies, which is designated as the *layer of ganglion cells.* In the neighborhood of the macula lutea of Man, two or three such cells lie upon one another, and at the yellow spot itself they form a layer several deep, displacing the nerve-fibre layer. The size of these bodies varies extraordinarily in one and the same retina.

Small ones, 15 μ in diameter, are to be seen lying in close contiguity to ones more than twice that size. All have the peculiar finely granular appearance of cell-substance as it presents itself in the nerve-bodies of ganglia and the central organs, generally without yellow pigmentation,§ which, as is well known, is often found in nerve cells. They contain a relatively large, homogeneous, transparent nucleus, and always that strikingly large nucleolus which ganglion cells everywhere possess, and within which a little vesicle or granule will occasionally be found. Notwithstanding the difficulty of isolating these cells without injury, quite a series of observations are at hand on the long and ramifying processes which they send out, after the manner of the ganglion cells of the central organ. In order to properly accomplish such an isolation, a condition of maceration peculiar and difficult to hit upon seems to be necessary, at least only thus can be explained the singular circumstance that the best preserved processes of the retinal ganglion cells which have yet been observed were taken from the retina of an Elephant, whose eyes were removed from the cadaver seven days after death.‖

The ganglion-cells with their processes may be seen in the fresh retina if we examine in serum the internal surface of pieces taken from the region of the ora serrata, the vitreous having been first removed. Between the scattered nerve-fibre bundles, which cross each other in many directions, are to be seen, quite superficially situated under the limitans interna, and in the plane of the capillary blood-vessels, numerous ganglion cells. These, with their processes, become more and more clear by gradually increasing pressure on the glass cover, and may be examined by the highest magnifying powers, careful manipulation being exercised lest the specimen should

* *Beiträge z. Mikr. A. w. Entwickelungsgesch. d. Rochen und Haie*, 1852, p. 24.

† *Z. f. w. Z.*, Bd. viii., p. 22.

‡ Graefe, *Archiv*, Bd. iv. 2, p. 41.

§ According to Corti, the ganglion-cells of the retina of the Elephant have a yellowish or yellowish-brown color.

‖ Corti, *Z. f. w. Z.*, Bd. v., 1854, p. 90, Taf. v.

become opaque by coagulation. Such, so to speak, still living ganglion cells (fig. 312, *A*) are of extraordinary transparency, since they contain in their cell substance only very minute granules, and consist essentially rather of an almost hyaline mass, in which lies embedded the completely hyaline nucleus with its brilliant and often finely serrated nucleolus. The already dead ganglion cells, and those changed by coagulation, present a totally different aspect, being coarsely granular and almost opaque; such may always be found at the cut edges of specimens prepared as above, or wherever else the specimen has suffered injury. A closer-examination of the living cells, with high powers, reveals the fact that the fine granules of the cell substance are partly arranged in lines and parallel rows, while the non-granular cell substance appears divided into fine striæ. The arrangement is exactly like that which I first described in the ganglion-cells of the brain and spinal cord.* The cell substance is probably fibrillated, and contains besides an inter-fibrillar granular substance, but the transparency of the living retinal cells is so great and the fibrillæ so fine that the microscopical picture is inferior in distinctness to that, for example, of the cells of the spinal cord. The fibrillæ nearest the nucleus approach a concentric arrangement; at the periphery, on the other hand, they pass into the processes which spring from the ganglion cells. In fresh preparations such processes may often be traced to several subdivisions, which may be of considerable size.

Where a process takes a straight course and has no ramifications, it cannot be distinguished, in respect to refractive qualities and finer organization,

Fig. 312.

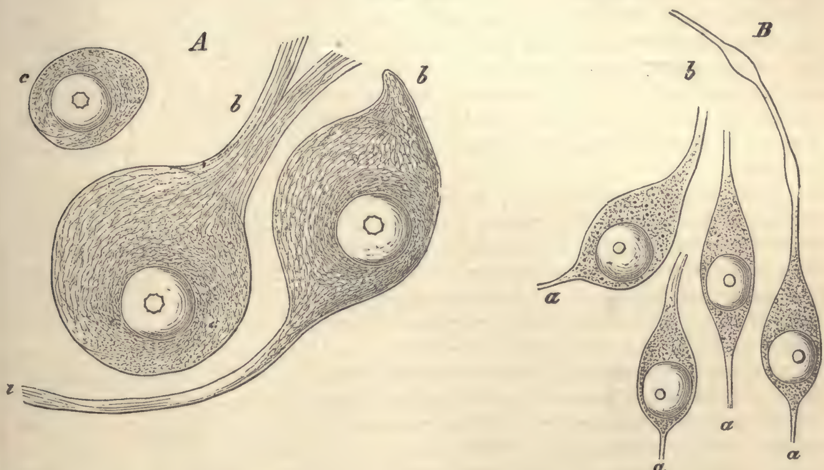

Fig. 312. *A*, Ganglion-cells from the fresh retina of the Ox, taken from the vicinity of the ora serrata, in situ; *a*, nerve-fibre process passing over into a bundle of optic-nerve fibres; *b b*, processes which lose themselves in the granular layer; *c*, small ganglion cells, such as are seen in great numbers lying next the large ones; *B*, ganglion-cells from the yellow spot in Man; *a*, centric, *b*, peripheric processes of the same. (×500.)

from the optic-nerve fibres, since these, as stated above, also possess the fibrillated structure. Reagents do not render this exceedingly delicate

* See this text-book, p. 135.

fibrous structure of the ganglion-cell substance more distinct; on the contrary, it disappears with the appearance of granular coagulation. Even iodized serum and osmic acid are ruinous to the transparency of the cells.

Of course no certain estimate as to the number of the processes of the ganglion cells can be formed by an examination of the surface of retinæ prepared as above. In many cells no processes at all are to be remarked, because they are crowded one upon the other or covered by the fibres of the opticus layer. Preparations by isolation and fine sections, so far as these methods have been useful in the study of the ganglion cells, go to show that the number of the processes of these ganglion cells, like those in the central organs, varies greatly. Cells with many processes have been delineated by preference, but there are also many cells with but two processes, as at the yellow spot (fig. 312, *B*). Unipolar cells have also been described.

Corti, as early as the year 1850, ascribed importance* to the similarity in aspect of certain of the ganglion-cell processes with the fibres of the optic-nerve layer, and relying upon the above-mentioned varicosities occurring in like manner in both, concluded that there was an immediate connection of the optic-nerve fibres with the ganglion cells. The uniformity in the phenomena presented by certain ganglion-cell processes and the nerve fibres of the retina was afterwards noticed by Remak, Hannover, H. Müller, Kölliker, and many others. The cells lie immediately next the layer of nerve fibres, in part embedded between the bundles of the same, and some of the cell processes, which are capable of being followed for a considerable distance, conform in every appreciable condition with the fibres of the optic-nerve layer: under the circumstances it is impossible to doubt as to the direct transition of the fibres into the cells. Whether *all* the fibres of the optic nerve communicate with ganglion cells *before arriving at the external layers of the retina* is another question. It may be that some of the diversities in the function of the optic-nerve fibres, which the physiologist is forced to admit, depend upon the existence or non-existence of a union between the nerve fibres and the ganglion cells. On this point no decision can at present be given.

According to a method proposed by Manz,† the opticus-layer of the Frog's retina, which has been prepared in alcohol, may be detached in such a way as to carry the ganglion cells with it:‡ thus the connection of the latter with the nerve fibres would be clearly demonstrated. The cells then appear for the most part unipolar. Manz takes for granted, however, that by this method of preparation the manifold peripheral processes which are preserved by other methods are torn away from their cells. We know, therefore, with regard to those processes of the retinal ganglion cells which do not disappear in the nerve-fibre layer only this much, that a portion take the direction towards the molecular layer. Anastomoses of the cells with one another by means of the thicker cell processes have been drawn by Corti from the retina of the Elephant. It is questionable whether such anastomoses, which have not been a second time observed, should be reckoned among the regularly occurring phenomena.

As in the case of the nerve-fibre layer, the radial supporting fibres form a framework between the ganglion cells: this will be hereafter described.

Division of the nervus opticus in animals is followed, according to W.

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* Müller's *Archiv*, 1850, p. 273, Taf. vi.

† *Zeitschr. f. rat. Med.*, Bd. xxviii., 1866, p. 231.

‡ H. Müller, *Zeitschr. f. w. Z.*, Bd. viii. p. 21, says with regard to the retina of Fishes: "If the nerve-fibre layer be raised up from the inner surface of the retina with the forceps, a portion of the cells readily follow with it."

Krause, by a fatty degeneration of the ganglion cells.* In eyes of blind persons, where anatomical examination reveals a disappearance of the nerve fibres, there is generally also an atrophy or a complete absence of the ganglion cells, as in cases of increase of intra-ocular pressure in glaucoma.

The *internal molecular layer* of the retina derives its appearance from a mingling of the finely-meshed network of connective substance, arising from the radial supporting fibres, with the delicate disappearing nerve fibrillæ. The latter, as Pacini† and Remak‡ first remarked, form a considerable portion of this layer. They may be isolated and traced for short distances in properly macerated retinæ, as exceedingly fine, smooth fibres, diversified with distinct spindle-shaped varicosities and many tortuosities. The larger and ramifying ganglion-cell processes which project into this layer, or belong to it from the first, may be more distinctly followed. Still, with regard to their final destination but little is known. While one portion of them is resolved into immeasurably fine fibrils, which may reach the outer layers of the retina only after many deviations, another portion, especially at the macula, appears to arrive at the layer of internal granules in the form of quite thick fibres. Such accounts are given, among others, by H. Müller,§ Kölliker,‖ Gerlach,¶ Manz** and Merkel.†† Owing to the diminution in resistance of the connective substance, the yellow spot of Man seems to be the most favorable place for tracing the nerve fibres as they pass into the molecular layer. But inasmuch as here the ganglion cells are nearly all bipolar, and in other places multipolar, the question arises, whether there may not also be great differences in the course of the processes. In general the same differences of opinion prevail with regard to the nature of this molecular layer, as with regard to the gray granular substance of the brain.‡‡ Especially is it doubtful, whether, besides the fine and finest nerve fibres and the fibres and network of the connective substance, there here exists a certain quantity of fine granules of unknown nature, as the appearance indicates; or whether the nerve fibrils and the spongy connective substance with their peculiar arrangement are sufficient to account for the finely granular appearance.

In regard to the career and final fate of the ganglion-cell processes and the fine nerve fibres of this layer, we must confess to the impossibility, so far as present researches go, of expressing any settled opinion, the macula lutea being excepted. The internal molecular layer interrupts our knowledge of the course of the nerve fibres, which is recovered in the more external layers of the retina. The thickness of the internal molecular layer in Man varies, according to H. Müller, between 0.03–0.04 mm.

The dark stripes which are to be seen in cross-sections of the retina of many animals, running parallel to the surface, and indicating an arrangement of the granular substance concentric with the tunics of the eye, have as yet no sufficient explanation. G. Wagner states that he has counted eight such layers.§§ The spongy connective tissue doubtless takes some part

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* *Membr. fenestr.*, p. 38.

† *Nuove ricerche sulla tessitura intima della retina.* Bologna, 1844.

‡ *Medicinische Centralzeitung*, 1854, No. i.

§ *Z. f. w. Z.*, Bd. viii. p. 61.

‖ *Icones physiolog.*, Taf. xix., fig. 12, λ

¶ *Gewebelehre*, 2 Aufl., p. 498, fig. 220.

** *Zeitschr. f. rat. Med.*, Bd. xxviii., p. 237.

†† *Macula lutea*, p. 11, fig. 9.

‡‡ Compare among others H. Müller, *Z. f. w. Z.*, Bd. viii., p. 115. Henle and Merkel, *Z. f. rat. Med.*, Bd. xxxiv., 1869, p. 49.

§§ *Sitzungsber. der Marburger. Naturf. Ges.*, *Juli*, 1868, No. 5, p. 47.

in this structure, since it is disposed in finer meshes in the course of these dark lines, as is demonstrated in my researches on the retina of the Roach.*

The *layer of internal granules*, which lies next external to the internal molecular layer, contains, as was already known to Vintschgau† and H. Müller, two different kinds of cellular elements, which are in communication with two different kinds of fibres having an essentially radial course. Besides the radial supporting fibres, which in this layer occupy an important space and communicate with each other by numerous filaments and interposed networks, there are many likewise radial nerve fibres, whose course exceptionally deviates from that of the radial fibres and is directed diagonally towards the surface of the retina.‡ These possess throughout the appearance and perishability of the fibres of theopticus layer, and are distinguishable from the harsh, finely indented supporting fibres by their spindle-shaped varicosities and smooth surfaces. Embedded in both kinds of fibres are spaces containing nuclei, and these constitute the so-called internal granules. The nuclei of the radial supporting fibres, which are much inferior to the others in point of number, will be described later; those which lie in the course of the nerve fibres, and owing to their great number arrange themselves in the form of several superimposed layers, resemble small bipolar ganglion cells. The quantity of their fine granular substance, however, is small, and the nucleus therefore relatively larger than in the real ganglion cell; the nucleolus is plainly visible in the homogeneous nucleus, but on the other hand is smaller than in the true ganglion cell. The more peripheric of the two processes belonging to the inner granules, which processes are no more or less than the radial nerve fibres, is commonly thicker than the centric one, as Merkel§ has described in his treatise on the region of the macula lutea. In animals also there appear generally to be but two processes arising from the internal granules,‖ but inasmuch as a good isolation of them is exceedingly rare, we are still very far from any definite knowledge with regard to the nervous inner granules and their processes, in the various regions of the retina of Man or animals. Some observers, for instance Ritter,¶ have described more than two processes. Great differences exist between certain of the inner granules. H. Müller affirms that in Man, as well as in Vertebrate animals generally, the more internal layers contain somewhat larger granules. W. Krause distinguishes, besides these two varieties and the nuclei of the supporting fibres, also a fourth variety of internal granules,** which form the outermost layer, and project into the external molecular layer (membrana fenestrata of W. Krause). These are said to be unipolar, having no connection with the outer layers

Fig. 813.

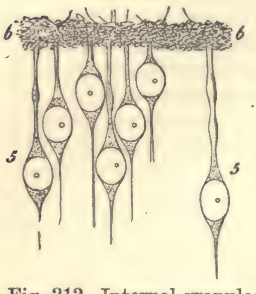

Fig. 313. Internal granules of the Human retina. × 800.

* *De ret. str. pen.*, fig. 5.

† *Ricerche sulla strutura micr. d retina dell' uomo, degli animali vertibrati e d. Cephalopodi. Sitzungsber. der Wiener Acad. d. Wissensch.* Bd. xi., 1853, figs. 1, 5, 6, 9.

‡ *Bei falco buteo*, M. Schultze, *A. f. m. A.*, Bd. ii., p. 262, and Hulke, on the Yellow Spot of Man, *Phil. Trans.*, 1868, p. 112.

§ L. c., p. 11.

‖ M. Schultze, *A. f. m. A.*, Taf. xiv., fig. 9. b, von der Katze. Hasse, l. c., p. 257.

¶ *Wallfischauge*, p. 37.

** *Membr. fenestr.*, p. 42.

of the retina,* and may be considered as the terminal organs of the nerve fibres.

Quite different is it with those cells, seen in certain animals, especially Fish, which project into the internal granule layer, and which are connected with the fenestrated inter-granular layer, as it was called by me (stratum intergranulosum fenestratum).† These are to be considered as a special development of the connective substance of the layer next to be described.

The thickness of the layer of internal granules in Man is 0.03–0.04 mm., according to H. Müller; it diminishes to 0.02 mm. at the ora serrata, where not more than three rows of granules remain, but increases to 0.06 mm. at the yellow spot.

The layer of internal granules is separated from the external granules by an inter-granular layer, being a thin stratum of finely-woven substance, in whose meshes are embedded a few nuclei and smooth cells, and in which coarser lines may be seen lying parallel to the retinal surface, and indicating a possible separation of the layer into still thinner subdivisions. In cross-sections of the retina of Man and the higher Vertebrates, this layer is represented as a finely punctate, granular stratum, which possesses a great similarity in appearance with the internal molecular layer, although much thinner than it. For this reason Henle gave to it the name *external molecular layer*, which we, as before stated, shall adopt, in order to avoid confusion with the inter-granular layer of H. Müller. W. Krause has recently brought into use the name membrana fenestrata.

The external molecular layer in its simplest form, as it appears in Man and the Mammalia, consists of a thin layer of granular substance which throughout the whole retina maintains about the same thickness, in Man, about 10 μ. In its finely-meshed groundwork of connective substance are embedded exceedingly fine fibrillæ, which run for considerable distances without giving out branches, and may take a course either diagonal or parallel to the surface of the retina. These fibrillæ, on account of their well-known fine spindle-shaped varicosities and their otherwise smooth contours, must be considered as nerve fibres, like their counterparts in the internal molecular layer. They are developed partly from the peripheric processes of the inner granules, partly from the fibres of the rods and cones. Some few nuclei are scattered throughout this layer, but they probably all belong to the connective substance, which in this locality in different animals presents manifold modifications; this subject will be discussed at length hereafter. Of the nerve fibres of this layer we know no more than of those in the internal molecular layer. They diverge from the radial course, and although, according to isolated observations, fibres have been seen passing directly through,‡ by far the greater number go to form in this plane of the retina a plexus so fine and complicated as appears only in the gray substance of the nervous centres.

The fibres of the rods and cones, which take considerable part in the formation of the external granule layer, arise by their inner extremities in the external molecular layer. All the so-called external granules represent nucleated enlargements of these fibres. The layer of rods and cones itself lies external to, and in immediate apposition with the layer of external granules, and is in continuous connection with the same by means of the

* Compare W. Krause's *Schema*, l. c., Taf. ii., fig. 1, gri.
† *De ret. str.*, 1859, p. 13.
‡ Hasse, *Z. f. rat. Med.*, Bd. xxix., p. 255.

above-mentioned fibres. A sharp boundary-line, as is seen in cross-sections of the retina separating the external granules from the rods and cones, is formed by the external limiting membrane.

In most portions of the Human retina and almost universally in animals the interspace between the limitans externa and the external molecular layer is only just sufficiently large for the disposition of the external granules, one nucleus for each rod and cone, not to mention the small quantity of connective substance which is also present in this layer. In this by far the most common case the external molecular layer may be truly considered as an inter-granular layer. In the posterior portions of the eye, however, especially in the region of the macula lutea of Man, the interspace between the limitans externa and the outer molecular layer becomes much more considerable in size. But instead of separating from one another, the outer granules still retain their position against the limitans externa, forming a tightly-packed compound layer; to the inside of this layer is thus left a free space, which is for the most part occupied by the fibres of the rods and cones as they pass towards the external molecular layer. Inasmuch as the entire space between the limitans externa and the external molecular layer has received the name "layer of external granules," there here exists an inner division of this layer, which is devoid of granules, and has been called by Henle the external fibre layer. It is worthy of mention in this connection that the rod- and cone-fibres are present throughout the entire layer of external granules, even where they are not indicated as a distinct layer by the designation external fibre layer.

Fig. 314.

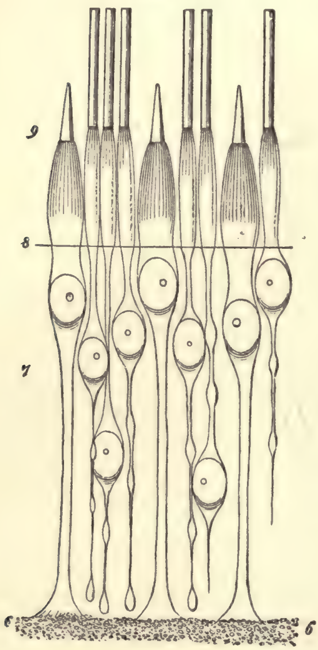

Fig. 314. From the posterior portion of the Human retina. 6, external molecular layer; 7, layer of outer granules; 8, limitans externa; 9, rods and cones, whose outer segments are sharply contrasted with the inner cylinders. (× 800.) The supporting fibres of connective substance are not indicated in the drawing.

The fibres proceeding from the cones are thicker than those proceeding from the rods, as is shown by the accompanying figure. Both are pale, having smooth surfaces, and both are very perishable, especially the thin fibres of the rods. Their disappearance in weak solutions of chromic acid or osmic acid is preceded by the appearance of varicosities, which increase in size with the weakening of the solution, and finally, by a general swelling of the whole fibre, cause its destruction. These phenomena agree perfectly with those which we have observed in the nerve fibres of the retina. Similar metamorphoses also take place in the thicker and more resisting cone-fibres as well as in the rod-fibres. This may be best observed where the cone-fibres are longest, namely, at the macula lutea. In moderately hardened preparations they present themselves as pale fibres with perfectly smooth surfaces, never branched or anastomosing, or passing over into sponge-like networks, and thus they are

sharply contrasted with the radial supporting fibres and the surrounding connective tissue. In fluids which cause prominent varicosities of the optic-nerve fibres the cone-fibres also are liable to the formation of distinct varicosities, which in the end lead to swelling and dissolution of the whole fibre (fig. 315). Finally, they resemble completely the thicker fibres of the opticus layer in the fact that with high magnifying powers they present the appearance of a fine longitudinal striation, and accordingly possess the indication of being composed of fine fibrillæ; this appearance we hold to be characteristic of all the thicker axis cylinders (fig. 316).

At the external molecular layer the cone-fibres undergo a peculiar variation in form. Each one possesses at the external limit of the above-mentioned layer a conical, triangular intumescence (fig. 314, 6, 6), beyond which the fibre as a whole can be no longer followed. *

Fig. 315.

Fig. 315. Cone and cone-fibre, the latter provided with varicosities; from the vicinity of the yellow spot of the Human retina. (× 500.)

These triangular enlargements of the cone-fibres are embedded in the substance of the external molecular layer in such a manner as to give the appearance of being continuous with it; and when they can be isolated they carry with them adherent shreds of the same layer, thus giving additional support to the idea of continuity. In fact the internal extremity of the cone-fibre resolves itself at this point into fine fibrils, which, however, are different from those of the network of the external molecular layer. In successful preparations of the Human retina, macerated in iodized serum, I

Fig. 316.

Fig. 316. Rod-fibres with and without varicosities, from the inner division of the layer of external granules of the macula lutea of Man. (× 1000.)

find these triangular enlargements to be resolved into pencils of numerous and exceedingly fine fibrils, which are not connected together in the form of a plexus.† If we compare this picture with that of the network of the external molecular layer, similarly hardened and isolated, the difference between the two kinds of fibres is strikingly apparent. This dissimilarity is

* H. Müller, *Z. f. w. Z.*, Bd. viii., Taf. i., figs. 1 and 3. Henle, *Eingeweidelehre*, p. 650. M. Schultze, *Archiv f. m. A.*, Bd. ii., Taf. x. and xi.

† Hasse (*Z. f. rat. Med.*, Bd. xxix., p. 252) thought that only three of these fibrils arose from a single triangular enlargement, while Merkel (l. c., p. 7) holds bifurcation to be the usual arrangement, at least at the macula lutea.

strengthened still further, in the first place, by the easily demonstrable connection between the network and the radial supporting fibres, and again by the manifold differences in appearance between the latter and the cone-fibres, since the tendency to the formation of varicosities which characterizes the cone-fibres, and indicates a relationship with the nerve fibres, is entirely wanting in the radial supporting fibres, which are distinguished by their peculiar rough surfaces. In this condition of affairs, the relation which the cone-fibres bear to the external molecular layer cannot tend to disprove their nervous nature, as assumed by W. Krause. *

With regard to the fibres proceeding from the rods, they also can only be followed as far as, or a short distance into, the external molecular layer. Our knowledge of their manner of termination is even more incomplete than that of the cone-fibres. The great fineness and frailty, especially of the inner half of the rod-fibre in Man and the Mammalia, account for the fact that only in exceptional cases a view can be obtained of the fibre in its entire length up to the external molecular layer. Very often the rod-fibre, especially when many varicosities occur in its course, terminates just before reaching the external granular layer in a large club-shaped expansion.† This gives the impression of a repetition in miniature of the dilatation of the cone-fibre which occurs at the same point, but I have been able to discover no such subdivision into fine fibrils as is characteristic of the cone-fibre. In Fish,‡ however, and still more in Birds and Amphibia,§ there remains no doubt on this point. In the last-mentioned animals the layer of external granules is formed for the most part by only two rows of granules, which are in communication with the external molecular layer by very short fibres. There is but little distinction here between the granules of the rods and cones, as well as between the fibres belonging to each, which at the outer molecular layer resolve themselves in like manner into fine fibrils. In Fish also, where the difference in the thickness of the longer rod- and cone-fibres is very plain, the expansions of the rod-fibres are very similar to those of the cone-fibres. In short, every circumstance goes to show that no essential difference, except in thickness, exists between the rod- and cone-fibres, and that the rod-fibres probably always divide into a number of fine fibrillæ at the external molecular layer, in like manner with the cone-fibres. It is true that in Man and the Mammalia the rod-fibre is very fine, but it always surpasses in thickness the finest optic-nerve fibrils, especially that portion which is more peripheral and approaches the limitans externa; this is always considerably stouter than the internal and more central portion, which is directed towards the outer molecular layer.

Each rod- as well as cone-fibre is in communication with a so-called external granule, that is, each of these fibres presents in some portion of its course an enlargement in which lies embedded a nucleus, and this is called the rod- or cone-granule (compare Fig. 313). If the fibres under consideration are nerve fibres, then the granules correspond with small bipolar nerve- or ganglion-cells. The quantity of cell substance is however very small, still somewhat more abundant in the larger granules of the cones than in those of the rods. The rod-granules are, except at the yellow spot, much more numerous than the cone-granules, and are disposed in several rows lying in close contact one above the other. The cone-granules lie close against

* *Membr. Fenestr.*
† M. Schultze, *A. f. m. A.*, Bd. ii., Taf. x., fig. 1. Hasse, l. c., p. 248.
‡ M. Schultze, *A.f. m. A.*, Bd. ii., Taf. xi., figs. 8 and 9.
§ Idem, figs. 18 and 19.

the membrana limitans externa, except where the cones are so crowded together, as at the macula lutea, that the granules belonging to them must necessarily be arranged in several superimposed layers.* Thus it happens that generally the cone-fibre is not interrupted by the cone-granule, but springs originally from it. The cone itself therefore is ordinarily attached directly to the cone-granule, while the rod communicates with the rod-granule, which does not lie in immediate apposition with the limitans externa, by a portion of the rod-fibre, similar in character but somewhat thicker than the portion which passes inwards toward the external molecular layer. This latter internal division of the rod-fibre is of course reduced to a minimum in length, according to the length of the peripheric portion of the same fibre in cases where the rod-granule is in direct apposition with the external molecular layer.

Fig. 317.

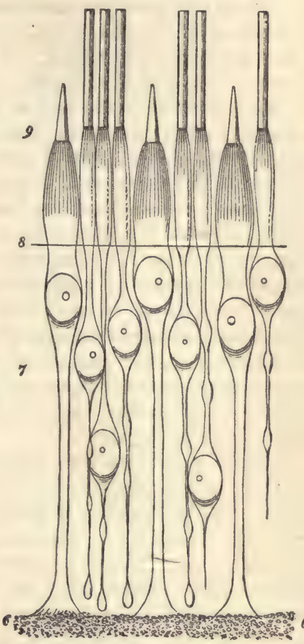

Fig. 317. From the posterior portion of the human retina. 6, external molecular layer; 7, layer of external granules; 8, limitans externa; 9, rods and cones, whose external segments are sharply contrasted with the internal segments. ×800. The supporting fibres of connective substance are not indicated in the drawing.

The rod- and cone-granules are in life entirely transparent, the differences in refractive power between cell-substance, nucleus, and nucleolus are exceedingly few; granular opacities are seen in them only after death as the result of independent coagulation or the influence of reagents. Thus the appearance described by Henle,† of transverse striæ or bands in the rod-granules, which may be seen in Man and the Mammalia sooner or later after death, and may be demonstrated in the clearest manner by treatment with diluted acids,‡ seems to be a post-mortem appearance, depending upon a separation of the nucleus or its contents. §

If the external granules are a peculiar kind of nerve cells inserted in the course of the nervous fibres, then still more must the *rods* and *cones* themselves be considered as the nervous terminal organs of the optic nerve. The anatomical connection is perfectly clear, in so far, that on the other side of the limitans externa a flask-shaped cone is derived immediately from each cone-granule;

* Exceptionally also in more peripheral portions of the retina, the transition from cone to cone-granule is longer. This peripheric portion of cone-fibre is in this case always thicker than the centric portion leading to the molecular layer. Compare Fig. 321.

† *Göttinger Nachrichten*, Mai and Novr. 1864, Nr. 7:

‡ M. Schultze, *A. f. m. A.*, Bd. ii., p. 219; according to W. Krause, *Membr. fen.* p. 32, also to be seen in the cone granules.

§ W. Krause, *Anat. d. Kaninchens*, p. 129. Compare also " On the still unexplained appearance of the transverse striæ," Ritter in Graefe's *Archiv*, Bd. xi., Abth. i., p. 89. G. Wagener (*Sitzungsber. d. naturwissensch. Ges. zu. Marburg*, 1868, No. 5) remarks that the transverse striæ appear in fresh preparations when examined with high powers, but not so sharply defined as with lower powers.

and a rod from each rod-granule either through an intermediate expansion of the latter, or directly, when the rod-granule lies close against the limitans externa. The layer of rods and cones, like a forest of compact palisades, covers the outer surface of the external layer of granules, and concludes the retina as nervous membrane. In it must take place the translation of the action of light into nervous action, which process ultimately lies at the foundation of the act of vision.

The rods are cylindrical; in Man, in the posterior portions of the retina 50–60 μ long and 2 μ thick; further forward towards the ora serrata they are somewhat shorter, but of the same thickness. They stand close to one another, so that between them but little more interval is left than is rendered unavoidable by their cylindrical form. Between the rods, however, at regular distances, which vary only at the macula lutea and ora serrata, are to be found in Man the flask-shaped cones. These stand on an average 8–10 μ distant from one another, and this interval between two cones is filled up by from three to four rods arranged in a straight line. The thickness of the cones, with the exception of those at the macula lutea, averages at the base 6–7 μ. They diminish in size externally after the manner of a wine bottle, being often somewhat thicker just above the base, and pass into a conical point, the end of which comes before the end of the rods, so that the cones are shorter than the adjacent rods. The cones, like the rods, become shorter as they approach the ora serrata, and increase rather than diminish in thickness.

In both structures two essentially different parts are to be distinguished, which have been called, by W. Krause,* external segment and internal segment. The distinction is most striking and has been longest recognized in the cones, to whose conical point, conspicuous by its high refractive power, H. Müller applied the peculiar name cone-rod. In the rods the conditions are analogous, except that the external segment is not conical but for the most part regularly cylindrical in form.† The dividing line between the inner and outer segment of the rod is, in the posterior portion of the human retina, not far from the middle of its whole length. I give as the measurement for each of the two divisions 25-27μ in length. The line of demarcation between outer and inner segment of the rods is for the most part in the same plane. For the cones, however, this plane is different, and lies in Man and the Mammalia further forward. The inner segment of the cone (cone-body) is therefore always shorter than that of the adjacent rod, the difference in length averaging 6 μ in the posterior portion of the human eye. It is not easy to estimate the length of the outer segment of the cones, owing to the great difficulty of preserving it from decomposition, and obtaining a view of it in the fresh and unchanged state. It appears to be the rule, however, that where cones and rods are to be seen mixed together, the external segments of the cones are always shorter than those of the rods. I give the measure 12 μ for the length of the conical outer segment of cones in the best possible state of preservation and taken from the posterior portion of the human eye, a measure which amounts to about half the length of the corresponding part of the neighboring rods. Great differences in this respect exist in different animals. In the Pig, for instance,

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* *Göttinger Nachrichten*, 1861, No. 2. *Zeitschr. f. rat. Med.*, 1861, Bd. xi., p. 175.

† In the Amphibia (the Frog, Triton, and Axolotl) the external segment of the rod decreases somewhat in diameter at its outer extremity. This is very marked in young animals especially (*A. f. m. A.*, Bd. iii., Taf. xiii., fig. 14), and may under some circumstances make the distinction between rod and cone impossible.

whose retina is extraordinarily rich in cones, the shortness of the latter in comparison with the rods is very apparent. In some places the cones with their outer segments scarcely reach the boundary line between the inner and outer segments of the rods. (See the accompanying figure.)

The differences of both divisions of the rods and cones as to their power of refracting light is perceptible even in the absolutely fresh state, but becomes plainer with the post-mortem changes, which set in very soon after death, and which the most careful manipulation cannot avert. These consist partly in finely granular opacities invading the originally homogeneous substance of the inner segment, which has a somewhat lower refractive power, while the outer segment retains its brilliant and homogeneous appearance. As a consequence of this change the dividing line between the two segments is more sharply marked. While the rods can be preserved in indifferent fluids for a certain length of time without undergoing further changes; the inner segment of the cones are generally very soon affected by a coarsely granular coagulation, which renders them more and more opaque, and the outer segments are in a short time entirely unrecognizable. Almost immediately after the preparation of a fresh specimen the outer segment becomes bent and distorted, and finally suffers a separation of its substance into thin laminæ, which hang together for a time, then swell up and disappear.

Fig. 318.

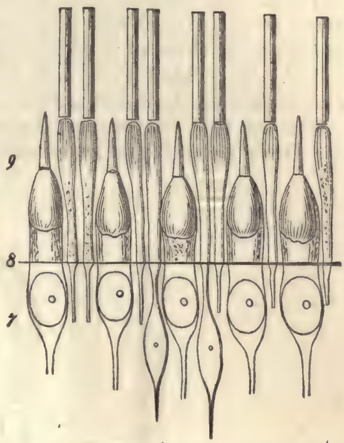

Fig. 318. Rods and cones (9), limitans externa (8), and portion of layer of external granules (7), from posterior portion of Pig's retina. The closely packed cones enclose within their internal segments a brilliant body of unknown signification. ×800.

The external segments of the rods also succumb to the same fate, although more slowly. The well-known peculiar changes, which these suffer when immersed in serous fluids, especially in serous fluids diluted with water, depend, as I have shown,* upon swelling, which at first reveals a regular transverse striation, and then often occasions a rapid division into laminæ. Inasmuch as the swelling often advances irregularly it causes curvatures and manifold variations in form of the outer segment, and generally leaves as final result a globular mass similar to certain myelin drops.

The large rods of the Frog, when isolated fresh in serum, always show in certain parts a very fine transverse striation, even with centric illumination and magnified 500–800 times. When such an appearance does not present itself, it may be rendered plainly visible by the use of very oblique illumination.† As soon as swelling takes place in the substance of the external segment, thin laminæ may be seen to separate themselves, until, under the influence of the serum, diluted with water, the substance of the laminæ themselves distends and the structure becomes totally unrecognizable. Exactly the same phenomena are to be observed in the rods of Man and

* *A. f. m. A.*, Bd. iii., p. 224.
† M. Schultze, *A. f. m. A.*, Bd. v., p. 380. Anm.

the Mammalia. But the highest powers and the use of oblique illumination are here indispensable from the first, before visible swelling and lengthening of the outer segment takes place. Thus the outer segments of the rods of Man and the Mammalia, which while still warm have been put into a 1–2 per cent. solution of osmic acid, and have preserved their form unchanged, show a striation, when examined with a power magnifying a thousand times, and with very oblique light falling in the direction of the longitudinal axis. These striæ are exceedingly fine, as if marked on copper, and almost equal in tenuity to those of Nitschia sigmoides, a diatom well known as a difficult test object. This corresponds to a separation of the lines of 0.03–0.04μ. The laminæ of the cones are somewhat thicker.*

Besides this thoroughly characteristic structure the outer segments, in the fresh or well-preserved condition, display a longitudinal striation.†

Fig. 319.

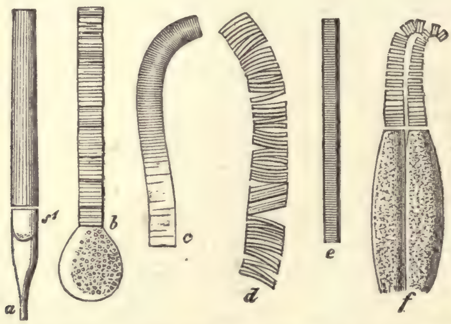

Fig. 319. External segments from rods and cones. *a–d*, rods from the Frog; *e*, from Man; *f*, double cone from a Fish (Perch); *a*, fresh and in connection with the inner segment, (s′ the lenticular shaped body); *b*, first stage of the swelling in serum; *c*, the same in diluted liquor potassæ, ×500; *d*, resolution into laminæ, in serum, ×1,000; *e*, from the human eye opened immediately after enucleation, and preserved 24 hours in strong perosmic acid, as seen with oblique illumination, ×1,000; *f*, fresh, in serum.

This depends, as Hensen first observed, upon a number of lines running lengthwise, either in parallels or long spirals, along the surface of the rod, but having some relation with a deeper differentiation in its structure. As it often happens in rods treated with osmic acid that by tearing, rubbing, or crushing of the preparation, laminæ are separated, sometimes thicker and sometimes thinner, which turn their flat surfaces toward the observer, it is not at all difficult to obtain a clear view of the relief of the superficies. In such laminæ may be observed, as shown in fig. 320, besides the grooving of the surface, also a suggestion of a radial division of the substance. Rods in the fresh state, and examined in serum show here and there longitudinal fissures. The character of the superficies of the laminæ, which reminds one of crenated blood globules, does not depend upon shrinking.

* Direct measurements are given by M. Schultze, *A. f. m. A.*, Bd. iii., p. 228, and W. Zenker, idem, p. 259. By the use of more perfect lens-systems I now obtain somewhat lower numbers than those there given. W. Krause's contradiction is found in *Membr. fenestr.* p. 23.

† Hensen in Virchow's *Archiv*, Bd. xxxix., Taf. xii., fig. 7. M. Schultze, *A. f. m. A.*, Bd. v., Taf. xxii.

The normal picture of a transverse section of the external segment in the fresh condition is exactly the same. I have shown that the longitudinal markings, which are more easily observed in Fishes and Amphibia on account of the greater size of the external segment, also occur in Man and the Mammalia, and probably in them also depend upon a grooving of the surface. This circumstance is in a high degree worthy of remark, namely, that the cross-section of the thick outer segment of the Amphibia (Triton) and Fishes (Sygnathus) often varies considerably from the circular form, and may be irregularly notched or even crescent-shaped.

Several observers have advocated the existence of an axial fibre running within the outer segment of the rod. Ritter's first description,* as well as the confirmatory observations of Manz † and Schiess,‡ gives room for the conjecture that the appearance of such a structure should be ascribed to the influence of the preservative fluids employed. When, however, the fresh

320.

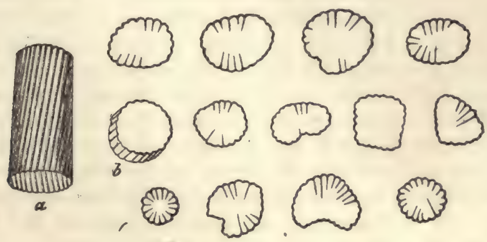

Fig. 320. *a*, external segment of rod from the Triton, fresh, in serum; *b*, thin lamina of the same, after treatment with a 2 per cent. solution of perosmic acid, broken off and viewed somewhat from the side. The remaining figures represent similar and even thinner laminæ from external segments of various thickness, and viewed from the surface. × 1,000.

retina of a Mammalian is viewed from above so as to command the still well-preserved ends of the rods, there may be sometimes seen, by varying the focal adjustment, a black point or short mark in the centre of the rod,§ and this appearance might be referred to the presence of an axial fibre. Hensen maintains with sound reasoning,‖ contrary to W. Krause's ¶ opposition, that it must relate to original structural conditions. An entirely satisfactory explanation of this phenomenon has not yet been given, for the successful demonstration by isolation of an axial fibre in the outer segment has not yet been made. Again not a trace of axial fibre or axial canal is to be detected in the detached laminæ, even in those of the thick rods of the Amphibia, no matter how perfect the state of preservation (see above). On the other hand, according to the observations of Zenker,** the differences in the index of refraction of the surface and the interior of the rods must be taken into account, and this may probably explain the appearance in question. Zenker estimates these indices at 1.5 as maximum and 1.33 as min-

* Graefe, *Archiv f. Ophth.*, Bd. v., 2, p. 101, Taf. iv.
† *Z. f. rat. Med.*, Bd. x., 1860, p. 305.
‡ Idem, Bd. xviii., 1863, p. 128.
§ M. Schultze *A. f. m. A.*, Bd. ii., p. 219. Taf. xiv., fig. 5. Hensen, in Virchow's *Archiv*, Bd. xxxix., p. 486. Taf. xii., fig. 4, A.
‖ *A. f. m. A.*, Bd. iv., p. 347.
¶ *Membr. fenestr.*, p. 23.
** *A. f. m. A.*, Bd. iii., p. 259.

imum.* In the rods of the Frog, somewhat swollen by perosmic acid, Hensen thought he recognized three axial fibres lying close together.†

Some observers accept the existence of an axial fibre also, in the internal segment of the rod.‡ W. Krause first described § such an arrangement in the cones of the Bird, where the fibre is said to terminate in an ellipsoid body, which was introduced under the name opticus-ellipsoid. We shall refer again to these bodies in the cones and rods of Birds and other animals, of which nothing is to be seen in the rods of Man and the Mammalia. The axial fibre of the inner segment, however, like the hypothetical one of the outer segment, is a very doubtful structure. In Human rods I have not been able to discover a single axial fibre.

The internal segments of the rods and cones of Man and many animals, show, on the other hand, by perfect preservation in perosmic acid, and examination with very high powers, a fine, longitudinal striation of the surface,‖ which reminds us of the above-mentioned external segments of the Amphibia, and which really is in part a continuation ¶ of the same. While in the case of the outer segments an independence of the striæ in the form of separable fibres is not demonstrable, the appearance being rather that of a simple superficial grooving (see above), the striation of the inner segments at least in certain places is due to fine separable fibrils. Upon the large cones of the human retina the striation of the surface is, under some circumstances, very distinct. The striæ run in the direction of the longitudinal axis or in lengthened spirals, and consist of about 40–50 single lines, everywhere equally distant from one another, being at the thickest part of the cone perhaps $\frac{1}{2}$ μ apart. At the point of the internal segment, the lines draw so near together that they can no longer be recognized singly, by our present aids to vision. Still the appearance is as if the striæ were prolonged upon the surface of the outer segment in the form of a conical tube. For a delicate sheath continuous with the striated cortex of the inner segment, may be isolated for a longer or shorter distance upon the outer segment. The rods in Man and the Mammalia, like the cones, present a superficial striping of the internal segment. The striæ run in the form of the finest lines, generally 8–10, at equal intervals around the inner segment parallel to the longitudinal axis, or, as on the cones, in a lengthened spiral, as far as the division between inner and outer segment. If the latter has fallen off, and the preparation has been well preserved in perosmic acid, there may be seen, projecting a little beyond the external end of the inner segment, and continuous with its striæ, a collection of exceedingly fine fibrils, forming as it were, a basket-work which formerly enclosed the external segment. In short there exists here as in the cones a fibre sheath for the outer segment, which is continuous with the striation of the inner segment, and which may be isolated for a certain distance. In spite of their fineness it is possible, even upon the highly refractive external segment of the rods of Man, to recognize the exquisitely fine lines which run straight or in faint spirals over the surface.**

As has been stated, these fibres are in part capable of being separated.

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* W. Krause.

† Virchow's *Archiv*, Bd. xxxix., p. 489, Taf. xii., fig. 8.

‡ Compare Hensen, *a. a. O.* fig. 6.

§ *Anatom. Unters.*, 1860. Taf. ii., figs. 5 and 6.

‖ M. Schultze, *A. f. m. A.*, Bd. v., p. 394. Taf. xxii.

¶ Hensen, Virchow's *Archiv*, Bd. xxxix., p. 489, made the first such observation in the Frog.

** M. Schultze, l. c. Taf. xxii., figs. 7–15.

Especially from the base of the cones of Man they become easily detached for a certain distance, and retain their position in the form of tubes standing upon the M. limitans externa after the cones have fallen off.* The limitans externa, viewed from the surface, then appears marked in finely dotted circles,† which correspond in diameter with the cones, and the appearance is as if the fibrils, which we regarded as composing the cone-fibres within the layer of external granules, ran singly over the surface of the cone-body. Were this the case the fibrils would be, in fact, nerves. This appears however, not to be so. Although the fine fibres are with difficulty traced backwards into the external granule layer, I have ascertained this much with certainty, namely, that they are continuous with the tissue lying between the fibres of the rods and cones. But since this tissue can only be considered as connective substance, the fibrils in question represent a continuation of the delicate fibrillated connective substance of the external granule layer, and form a supporting fibrillar frame-work for the bases of the rods and cones (comp. fig. 326).‡ Their further relations with the surface, especially of the cones of Man, are doubtful, by reason of a new complication in the structure of the interior of the cone-body. Here is to be found, according to my researches, a thick mass of fibrils running in the longitudinal direction and occupying the entire thickness of the cone-body so that a distinction between the superficial and subjacent fibres has not yet been successfully made. These internal fibrils, it is worthy of remark, do not descend as far as the limitans externa, but stop suddenly at a certain distance above it. Here at least they become invisible, and must change their character if they reach further—for instance, into the cone-fibre. Some cones are to be found, which, at the place where the internal fibrils stop, contain little globular masses like drops of fatty matter; others, which are here transversely broken off. In the fresh state the fibrillar portion of the interior of the cone presents itself as a brilliant, highly refractive division of the cone. It is possible also by proper maceration to isolate these fibrils. They terminate at the point where the outer segment begins. The union of the outer segment with the inner segment appears to be effected by a sheath, which also surrounds the fibrillar substance.

Fig. 321.

Fig. 321. Rod and cone from Man after preservation in a 2 per cent. solution of perosmic acid, showing the fine fibres on the surface, and the different lengths of the internal segment. The external segment of the cone is resolved into laminæ which still hold together. ×1,000.

* I formerly sketched very incomplete portions of these fibres (*A. f. m. A.*, Bd. ii., Taf. xi., fig. 13 *a*). They were introduced by W. Krause, under the name "needles," as special elements of the rod and cone layer (*Membr. fenestr.*, figs. 4, 5, 21).

† *A. f. m. A.*, Bd. v., Taf. xxii., fig. 6.

‡ Landolt has lately described a sheath-like prolongation of the connective substance over the rods in Amphibia (*A. f. m. A.*, Bd. vii., p. 94), which may correspond in its essentials with the above-mentioned fibrillar frame-work.

I recognize also in the interior of the inner segment of the rod in Man a precisely similar structure consisting of stiff fibrils (fig. 322, *A*, *ss*). The structure is throughout similar to that of the cones, and confirms the in other respects well authorized opinion, that between rods and cones, with the exception of the varying thickness of their respective nerve fibres, there exists no essential difference beyond that of size and form; that therefore both kinds of percipient elements are only modifications of one primitive form.

Fig. 322.

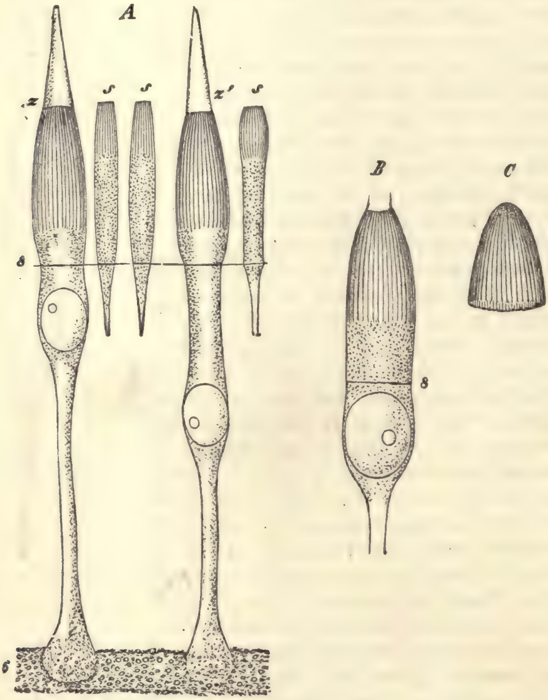

Fig. 322. *A*, inner segments of rods (*sss*) and cones (*zz'*), from Man, the latter in connection with the cone-granules and fibres as far as the external molecular layer, 6. The cone, z', is distinguished by an uncommonly long band running to the cone-granule (the thicker and more peripheric portion of the cone-fibre). In the interior of the inner segment of both rod and cone the fibrillar structure is visible. × 800. *B*, inner segment of a cone with cone-granule and beginning of the cone-fibre, from Man, in which the internal fibrillar structure does not descend so far towards the limitans externa. × 1,200. *C*, detached fibrillated portion of a cone from its interior, and therefore shorter than the cone itself, from a cone in the vicinity of the ora serrata.

With the rods and cones we arrive at the end of the expansion of the optic-nerve fibres in the retina. If we review again the connection of the nervous elements of the human retina, as we are enabled to present it in the present state of our knowledge, we find in the first place (compare the accompanying diagrammatic figure) the non-medullated nerve fibres of the opticus layer in connection with ganglion cells. At the macula lutea, where this union is particularly easy to be traced, these ganglion cells are all bipo-

lar. The peripheric process is the thicker, and passes into the internal molecular layer, there to ramify. In the other portions of the retina most of the ganglion cells seem to be multipolar, in which case probably one centric process runs to the opticus layer, the others, peripheric, are distributed in finest ramifications to the internal molecular layer. The nature and course of the fine ganglion-cell processes in the internal molecular layer resembles in every respect that of the finest primitive nerve fibrils of the gray cortical substance of the brain. They form in their complicated course the closest network, and lie embedded in the tough sponge-like connective substance, which hinders their isolation for any considerable distance. There is therefore but little chance that the communication of these ganglion-cell processes with the nervous fibres of the following layer can be demonstrated. In the layer of internal granules we find nerve fibres running perpendicular to the surface of the retina. At the macula lutea only are to be found fibres of this nature running diagonally to the surface. Each of these fibres is interrupted by a small cell, an internal granule, a bipolar ganglion cell, whose centric process (that portion of the radial nerve fibre which ascends from the internal molecular layer) is very fine, while the peripheric process is somewhat thicker. This latter loses itself probably through ramifications in the external molecular layer. These ramifications resemble those of the internal molecular layer, and like them render impossible a closer following of the nerve fibrils which traverse this layer. Here the rod- and cone-fibres take their origin, and follow a direction perpendicular to the surface, except at the macula lutea where they take a diagonal course. The cone-fibre is formed by the concurrence of a great number of fine fibrils, and presents the appearance of a thick fibre of the opticus layer; it is continuous with the nucleated cone-granule—a bipolar ganglion cell whose peripheric process is generally in fact the cone-body itself. If, as often occurs especially at the macula lutea, a longer interval remains between the cone-granule and the cone-body, this peripheric portion

Fig. 323.

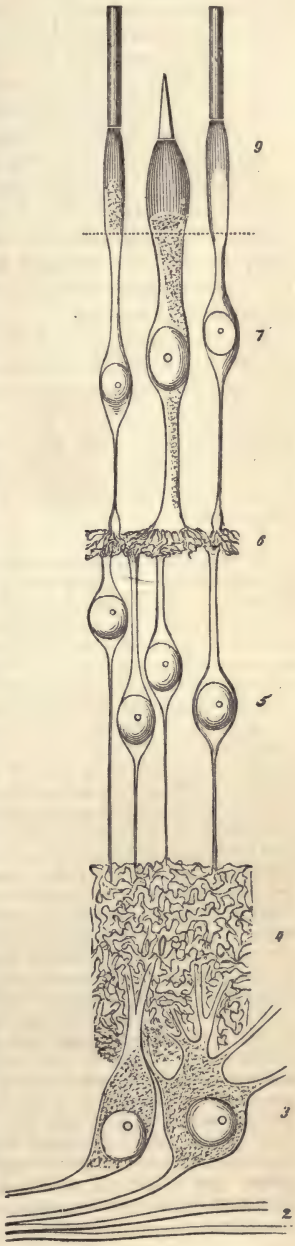

Fig. 323.—Diagrammatic representation of the connection of the nerve fibres in the retina. The numbers are the same as in fig. 310, p. 803. 2, opticus fibres; 3, ganglion cells; 4, internal molecular layer; 5, layer of internal granules; 6, external molecular layer; 7, layer of external granules; 9, rods and cones.

of the cone-fibre is thicker again than the centric portion. The rod-fibres are very much finer than the cone-fibres. Whether they also are composed of many fibrils has not yet been demonstrated, but is for several reasons probable. The peripheric portion of the rod-fibre is far thicker than the centric portion, which arises at the external molecular layer by an intumescence, analogous, and in many animals exactly similar, to that of the cone-fibre. The rods and cones themselves we regard as the terminal organs of the optic-nerve fibres. Whether the fibrils in the interior of the inner segment are continuous with the nervous fibrils of the corresponding fibre, and so represent its terminal modification, must remain undecided, as well as the question concerning the relations of the outer segment to the nerve substance. It is highly probable that the inner and outer segment have a common envelope, but every other method of continuity between them, for instance by interior nervous fibres, is a bare hypothesis. Possibly, therefore, the nerve substance might terminate with the inner segment, while the outer segment should represent a physical auxiliary apparatus, non-nervous in character.

The circumstance that the processes of the retinal nerve cells are always thicker towards the periphery than towards the centre (as represented in fig. 323) is very important, and worthy of remark in its bearing upon the signification of nerve cells in general. If the difference in thickness depended on the varying number of elementary nerve fibrils, the latter would be more numerous at the periphery than at the centre, which could only be explained by an increase in the number of fibrils within the nerve cells themselves.

The minutiæ in the anatomy of the rods and cones of the retina must excite our liveliest interest, when we consider that we have to do with structures whose office is to translate the phenomena of light into those of nervous conduction.

We can and must presume that the structure of the terminal organs is consistent with their function; and the hope of discovering something of this kind with the microscope draws near, and with reason increases from the fact, that the more exact the examination and the stronger the magnifying power, the finer and the more remarkable the structural details discovered. Well may this hope appear to many too bold on account of the shortness of the undulations of light. If, however, we consider more exactly that the measurements in question (namely, $0.7\ \mu$ for the approximate length of the waves of light at the visible red end of the spectrum, and $0.4\ \mu$ at the visible violet end) lie within the measurements appreciable and definable by the microscopist, we can no longer designate the task as too bold. In its pursuit the researches in comparative anatomy will naturally be of the highest value. However different the formation and development of the eyes of animals may be in general, still, for the purpose of transferring the undulations of light to the domain of nervous conduction, we may assume a conformity in the structure of the terminal nervous organs and their auxiliary apparatus, such as we see for instance in the organ of hearing, in the form of auditory filaments projecting into a fluid. Here then it may be allowable to present a short sketch of our knowledge of the terminal apparatus of the optic nerve in the lower animals, accompanying it with a hint as to the physiological value of the differences which present themselves.

All the Vertebrata that have the power of vision, perhaps with the single exception of the Amphioxus, whose eyes stand very low in the scale of development, possess a retina with a layer of rods and cones like that of Man. While generally the cones are recognizable by their club-shaped inner segment and conical outer segments, and are easily distinguished from the rods when the two are mingled together, as in the human retina (also in the Ape, the Pig, the ruminants, and most bony fishes), cases also occur in which the cones are more like the rods; thus in the Guinea Pig or Rabbit the inner segment of the cone is scarcely thicker than, or otherwise differently formed from, that of the rod, so that a distinction can be made only by the outer segment. But here also variations occur, as in the Triton,* and less distinctly in the Frog, where

* M. Schultze, *A. f. m. A.*, Bd. iii., p. 237.

the outer segment of the rod is conical in shape. In birds very thin rod-like cones are to be found, in which the conical form of the lengthened outer segment is not always easily apparent. If from this it would seem as though the sharp distinction between rods and cones disappeared in the animal kingdom, nevertheless there are always present certain marks which render the distinction possible in almost all cases. To these extraordinary marks belong in birds the highly refractive globules of fat-like substance, which generally have a yellow or red color, and exist in all the cones, while in the rods they are wanting. These lie in that portion of the inner segment where it passes over into the outer segment, and are of such a size that each one fills up that part of the cone in such a manner that no light can reach the outer segment without passing through the globule (see Fig. 324, *z*). There exist colorless globules of this kind, the greater part, however, are yellow, bright yellow, greenish yellow, gamboge, and orange; between these at regular intervals stand the ruby colored globules.

These globules must, by virtue of their sphericity, exert some influence on the course of the luminous rays, and according to their color absorb certain rays. Their presence proves, as Hensen first brought to notice,* with a high degree of probability, that the outer segment is the medium of perception, since otherwise the selection by absorption would be without purpose. The fact that they occur in the cones and not in the rods demonstrates that the former are more concerned in the perception of colors than the latter, which seems on other grounds to be the case in Man and the Mammalia.† That the globules in question occupy the entire thickness of the inner segment proves on the other hand, as Krause rightly observed,‡ that there exists here an interruption of continuity, and that the outer segments cannot be of nervous nature, even though the inner segments may be. I at one time believed it possible to point out the way in which the outer segment might take a share in the act of perception, namely by means of the fibres, discovered by me, which run over the surface of the inner segment and are continued upon the outer segment.§ The new complications, which the discovery of the internal fibre-system of the rods and cones introduces to this subject, prevent any decisive expression of opinion at the present time.

As in the Birds, the globules are found also in the cones of the Reptiles, sometimes colorless, in the Turtle red, orange, and yellow. Finally the very small cones of the tailless Batrachians are distinguished, each by a strongly refractive globule which is either colorless or bright yellow. They do not occur in the Fishes, unless the statement of Leydig in regard to the percipient elements of the Sturgeon ‖ has reference to them. Besides the colored globules, many cones in Birds (the dove) and Lizzards contain also a diffused red or yellow coloring matter, which may assist the globules in their office of elective absorption.

Besides this, another distinctive mark is to be found in the inner segment of the cones of the Amphibians, Reptiles, and Birds, also in the inner segment of the rods of the two last-mentioned classes; this consists in a lentiform body of stronger refractive power than the surrounding parts, and seems suited to exert some influence over the rays of light. In the rods it occupies the end of the inner segment, and is flattened posteriorly towards the outer segment, spherical or ellipsoidal anteriorly. In cones which contain the globule it is applied immediately to the anterior surface of the globule. W. Krause first saw this body in the cones of the Chicken and thought it should be considered as the knob-shaped end of the central nerve fibre of the inner segment, and gave it the name opticus-ellipsoid.¶ I have described it as the lentiform body.**

Perosmic acid applied to fresh retinæ makes the lentiform body, for instance in Birds and the Amphibia, exceedingly distinct, since it preserves the forms perfectly and brings out faint differences in color. In human rods and cones, whether fresh or with the help of this reagent, it is impossible to bring to view a similar body. It is worthy of remark that in some animals the lentiform body of the rod is composed of two parts which behave differently when treated with perosmic acid, and possess a different refractive power.††

In the rods of the Bird a small anterior section in the form of a short appendix, is

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* Virchow's *Archiv*, Bd. xxxiv., p. 405.

† M. Schultze, *A. f. m. A.*, Bd. ii., p. 253.

‡ *Membr. fenestr.*, p. 48.

§ *A. f. m. A.*, Bd. v., p. 400.

‖ *Anatom. histol. Unters. über Fische und Reptilien*, 1853, p. 9.

¶ *Göttinger Nachrichten*, 1867, No. 37.

** M. Schultze, *A. f. m. A.*, Bd. iii., p. 221.

†† M. Schultze, *A. f. m. A.*, Bd. v., p. 401, 403, figs. 2 and 17.

often separated from the point of the ellipsoidal lens.* This section is more brilliant than the rest of the lentiform body (fig. 324, *s'*). In the Triton the posterior section presents on its anterior surface a spherical concavity in which lies the anterior section in the form of a convex lens (fig. 324, 5 *c'*). It is natural to assume that we here have to do with a mechanism, which in a very decided way diverts from their course the rays of light which pass towards the outer segment.

Fig. 324.

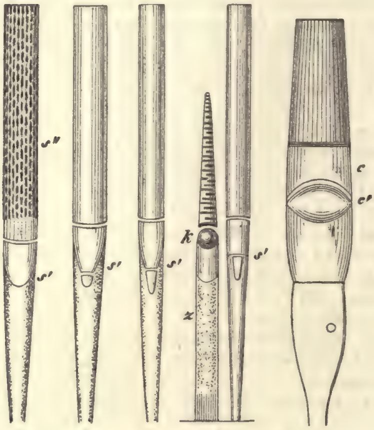

Fig. 324. 1, 2, 3, rods from retina of the Hawk; *s'*, inner segments with refractive lentiform bodies; *s''*, outer segment surrounded with pigment granules arranged in rows, as they often adhere to the outer segment in preparations hardened in perosmic acid; 4, rod and cone (*z*) from the Chicken; *k*, yellow globule in the inner segment of the cone, also an ellipsoidal refractive body; 5, rod from Triton; *c*, plano-concave; *c'*, biconcave lens in inner segment. ×800.

The twin cones or double cones, first described by Hannover,† are perfectly unintelligible in their physiological relations. In Man and the Mammalia they have not yet been observed,‡ but they occur in Birds, Reptiles, Amphibia, and Fishes. In Fishes, where they are largest, most frequent, and therefore easiest to find, they consist of two apparently precisely similar cones grown together, with separate outer segments and cone-fibres, so that one might suppose that they were cones multiplying by division in the longitudinal axis. It is otherwise with those animals, in whom as I have shown, essential differences exist between the two halves of the double cone; this cannot be without physiological significance. In Birds, Turtles, Lizards, and the Frog, in whom each cone commonly contains a colored or colorless globule, such a globule is found only in one half of the double cone; the other half contains only the ellipsoidal lentiform body, which in many Birds is colored yellow, but which even then differs essentially in form and refractive power from the colored globule of the other half of the cone.§ Very often there exists also a difference in length of the halves in such a manner that the one containing the globule reaches further back than the one without it, so that the planes in which the inner and outer segments come together do not coincide. If we consider the outer segment as the point of distinct vision, there would ensue the necessity of a different accommodation for each half of the double cone, that is, if they had the same functions and received the rays of light

* It was this appendix, which I formerly pointed out in swollen inner segments as being possibly the remains of a resistant axial fibre (*A. f. m. A.*, Bd. iii., p. 245, fig. 5).

† Hannover, *Recherches microscopiques*, etc., 1841. Details on this subject by M. Schultze, *A. f. m. A.*, Bd. iii., p. 231.

‡ Hannover thought he had found them, but was in error.

§ *A. f. m. A.*, Bd. iii., Taf. xiii., fig. 6, c.

under otherwise similar conditions. The latter, however, is not the case, inasmuch as the refractive lentiform bodies of the inner segment of the two halves are essentially different.

From all this may be drawn the conclusion, that the lentiform body is destined to give the rays of light such a direction for the final elaboration in the outer segment, as they seem incapable of receiving from the coarser refractive apparatus.

The variety in the distribution of the rods and cones in the animal kingdom is worthy of remark. Either form of percipient element may be represented by the other. Thus the retina of the Roach, the Shark, the river Lamprey, and probably the Sturgeon * is entirely wanting in cones; also among the Mammalia, the Bat, the Hedgehog, and the Mole; † while the retinæ of many Lizards, Snakes, Turtles, and probably all Reptiles, are without rods, containing exclusively cones. ‡ In Birds the number of cones is generally very much greater than that of the rods, while in the Mammalia the reverse holds true. In the retina of Man and the Apes the cones outnumber the rods only at the yellow spot, and at the centre of this region of distinct vision the rods are entirely wanting. In respect to the distribution of cones, the retina of the Bird in its whole extent possesses a similarity with the macula lutea of Man, which is augmented by the fact that the yellow globules of the cones hold a similar relation to the outer segments with the yellow pigment in the most sensitive portion of the human retina.

It is a remarkable fact that the number of cones is considerably less in the Owls, which fly in the twilight or at night, so that here again the rods are more numerous than the cones. In these Birds, also, the intensity of the yellow pigment in the cones is less than in the day Birds, but the red pigment is entirely wanting. § Likewise in Mammalia that prefer twilight or night to day, the cones are either markedly diminished in number, or entirely absent, as in the Bats and the other animals mentioned above. In the Rat, the Mouse, the Dormouse, and the Guinea-Pig the cones, if they exist at all, are only quite rudimentary in comparison with those of Man, the Ruminants, the Pig, and the Dog. The Cat possesses distinct but thin cones; in the Rabbit they are less distinct. ‖

It is worthy of note also that the absolute length of the outer segment of the rods is in most nocturnal animals very considerable. ¶ The number of the laminæ increases also with the length of the outer segment, but their thickness varies little if at all. According to this the reflection and elaboration of the luminous rays, in so far as they are affected by the laminated structure, will be more perfect when the outer segment is longer.

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* A more careful examination is necessary for the Petromyzon. I recently had the opportunity of examining the eye of the river Lamprey, and found in the rod- and cone-layer only one form of element, which, from the appearance of the outer segment, I took to be rods. According to an incidental observation by H. Müller (*Auge des Chamäleon*, p. 25), rods and cones are found mingled in the eye of the Petromyzon Marinus. According to Bowman (*On the Eye*, p. 89), and Leydig (*Fische und Amphibien*, p. 9) the Sturgeon possesses but one kind of percipient element, and these, according to Leydig's drawings, resemble the rods in the form of their outer segments. In the bony Fishes a mixture of rods and large cones is the rule. Among a great variety of Fish from the Baltic Sea, which I examined with reference to the distribution of the rods and cones, and among which were specimens of Pleunorectes, Gadus, Gasterosteus, Trachurus, Cottus, Crenilabrus, and Sygnathus, I found only in the latter notable deviations from the ordinary type. The rods are here very thick and short, as in the Amphibia, the cones are few in number, and the laminæ, into which the rods resolve after being hardened for a short time in perosmic acid, often have a well-marked crescentic form, similar to that which I have described in the Triton.

† *A. f. m. A.*, Bd. ii., p. 198, Bd. iii., p. 238.

‡ Idem, Bd. ii., p. 209. W. Krause's statement that in Lacerta agilis rods are present as well as cones, is erroneous. Hulke, as I have shown, has not been fortunate in discriminating between the rods and cones of Reptiles, so that his statements must be received with caution.

§ Compare my statements in *Archiv f. mikr. Anat.*, Bd. ii., p. 208, which after repeated researches I must hold to in every particular, notwithstanding W. Krause's opposition (*Membr. fenestr.*, 1868, p. 29).

‖ M. Schultze, *A. f. m. A.*, Bd. ii., p. 197; W. Krause's reply, see *Anatomie des Kaninchens*, p. 129 and *Membr. fenestr.* p. 30.

¶ M. Schultze, *A. f. m. A.*, Bd. ii., p. 199, Taf. xiv., fig. 7 (Rat), p. 208, Taf. ix., fig. 10, 11 (Owl), Bd. iii., p. 243, W. Krause, *Membr. fenestr.* p. 31.

The retinal structure of the Invertebrates differs essentially from that of the Vertebrates in accordance with the dissimilarity in development. This is especially evident in the percipient layer, or the layer of rods and cones. In Mollusks, Articulate Animals, and Worms the terminal extremity of the optic nerve presents, as in the Verbrates, a layer of palisade-like structures. These, however, are situated differently from those in the Vertebrates, being turned toward the light and looking forward in the direction of the lens, while in the Vertebrates the rod-layer lies in apposition with the choroid. This condition of affairs finds its explanation in the development of the retina, which in the Vertebrates is formed by a protrusion of the cerebral vesicle (see below); in the Invertebrates,[*] on the other hand, by an inversion of the skin.

Among the Mollusks we are most familiar with the retinal structure of the Cephalopods and Heteropods.[†] In the Cephalopods rod-like pallisades of considerable length, reddish in color to the naked eye, form the innermost layer of the retina, which is separated from the external layers by brownish-black pigment. The rod-layer is composed, firstly, of lamellated palisades after the manner of the outer segment of the Vertebrates, but much more diverse in the form of the transverse sections, which may be crescentic, round, four-cornered, or quite irregular. Neighboring palisades also may grow together in such a way as to present a coherent mass pierced by perpendicular tubes. The laminæ which compose these pallisades have, according to my measurements, nearly the same thickness as in the Vertebrates, that is, about $0.5\,\mu$; secondly, in the intervals between the palisades and on their surface are to be found fine nerve-fibrils, the terminal ends of the opticus fibres. These proceed into the rod-layer from a layer of nucleated fusiform cells, which may be compared with the layer of external granules. The nucleated spindles, however, which terminate in one direction by filaments passing into the rod-layer, are at the other end resolved into fine fibrils, which spring from the opticus layer. Thirdly, the rod-layer contains brownish-black granular pigment matter. This is never wanting at the outer end of the rods, and separates them from the spindles. This pigment lies, like the nerve fibres, external to the lamellar palisades, and surrounds them; then it stretches into the intervals between the palisades, where the nerve fibres ramify, and often forms at the inner end of the rods, where these are separated from the vitreous by a homogeneous membrane, a compact mass filling in the spaces between the palisades. Light can penetrate the latter, but is shut out, by the dense deposit of pigment, from the canals containing the nerve-fibrils, and can only reach them by a roundabout way through the lamellar palisades. (Compare especially M. Schultze, *A. f. m. A.*, Bd. v. p. 15–18.)

It is evident that if in the Vertebrata nerve fibres existed within the outer segments of rods and cones beneath the fine fibrils running on the surface, their situation in relation both to the lamellar substance and to the pigment of the retina would be exactly like that of the analogous structures in the retina of the Cephalopods.

In the Articulate animals the structure of the retina is complicated in accordance with that of the eye, which is compounded of many single eyes.[*] But here also are to be found behind the refracting media, which are represented by the cornea, lens, and vitreous body, lamellated rods,[†] which are endowed with extraordinary powers of refraction, and are often of considerable length. These rods are also surrounded by dark pigment, and are most intimately related with nerve-fibrils, which proceed from the opticus layer and terminate in or upon them. The division into lamellæ is here often perceptible even with the lower powers, as for instance in the Crab, for the thinnest disks, not more than $\frac{1}{2}\,\mu$ in thickness, are united in groups which present a peculiar appearance, and are recognizable by their color. The closer relations of the nerve-fibrils to the laminated rods is here less exactly understood than in the Mollusks.

Among the Worms, finally, there exists, at least in the large-eyed Alciope, an anal-

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* Semper, after a communication from Hensen, *A. f. m. A.*, Bd. ii. p. 416.

† Compare Babuchin, *Würzb. nat. Zeitschr.* Bd. v., 1864, p. 125; Hensen, "Ueber das Auge einiger Cephalopoden," *Zeitschr. f. w. Z.* Bd. xv.; and Bronn, *Klassen und Ordn. d. Th. Mollusken*, Taf. 115; Steinlin, *Beitr. z. A. d. Ret.* St. Gallen, 1865–66, p. 70. M. Schultze, *A. f. m. A.*, Bd. v. p. 1. On the retina of other Mollusks, among others, Babuchin, *Sitzungsb. d. Acad. zu Wien*, Juni, 1865, and Hensen, *A. f. m. A.*, Bd. ii. p. 339, where the entire literature is to be found.

‡ Leydig, *Das Auge der Gliederthiere.*

§ M. Schultze, *Untersuchungen über die zusammengesetzten Augen der Krebse und Insecten*, Bonn, 1868.

ogy in the formation of the rod-layer with the arrangements in the higher animals. So far as could be judged by preparations sent from Naples in preservative fluid, the rods, which were first observed by Krohn, have the appearance of highly refractive palisades with transverse striations. They were in part tubular, and plugged with pigment anteriorly, and were easily broken in a transverse direction. It is reserved for future observations to explain in what method the nerve-fibrils pass from the optic-nerve layer, which lies posterior to the palisades, and terminate in the pigmented layer of rods.

Here also we may mention that of late manifold doubts have been expressed as to the signification of the rods and cones as terminal organs of the optic-nerve fibres. The fibres of the rods and cones are said to be of the nature of connective tissue, and continuous with the connective-tissue cells and fibres of the internal layers of the retina. This is the opinion of W. Krause (*Membr. fenestr.* p. 48), and also in a certain sense of Landolt, in speaking of the Amphibia (*A. f. m. A.*, Bd. vii. p. 84). In Frogs, Tritons, and Salamanders the layer of outer granules, as has been shown, is of such small extent, and contains, besides the fusiform rod- and cone-granules, only fibres so short as to be of little use in deciding the question in point. Besides this, Landolt admits that the fibres in question may contain nerve fibres within them. The case is similar in Birds and Reptiles. In Mammalia and Man, to whom Krause's statements refer, the difference between fibres of the connective tissue and nerve fibres is so great, and the identity of rod- and cone-fibres with nerve fibres so convincing, according to the description given above, that it would be impossible upon anatomical grounds to doubt the nervous nature of the rods and cones. Further researches must explain why, in division of the opticus, which was practised on animals by W. Krause, and in certain cases of atrophy of the optic nerve and ganglion cells, the rods and cones were found not to have undergone degeneration. In any event the fact of their persistence will be unable to overthrow the anatomically and physiologically well-grounded supposition that the rods and cones represent the terminal organs of the optic-nerve fibres. This opinion holds good also on the grounds which Manz, in a very meritorious work on the eye of the acephalous abortions, recently urged against the nervous nature of the rods and cones. The presence of the latter in the hemicephali proves only that the elements of the external retinal layers may under certain circumstances be developed independently of the internal layers; and this, if we consider the rods and cones as nerve-ends, is in complete accordance with what we find in other nerves, whose peripheric terminal organs may be well developed while the central organ is wanting.

2. The Pigment-Layer of the Retina.

The Layer of Pigment Cells, which is generally described as the pigmented epithelium of the choroid, belongs both in a physiological and morphological point of view to the retina, although, so far as is known, it is in no

Fig. 325.

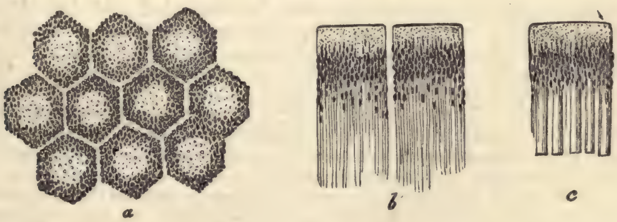

Fig. 325. Cells from the pigment layer of the human retina. *a*, surface view, cells united together; *b*, viewed from the side with long hair-like processes, partly pigmented, partly without pigment; *c*, a cell viewed also from the side to which outer segments of the rods adhere.

sense continuous with the nerve fibres. This layer is formed during the period of embryonic development from the external membrane of the primitive ocular vesicle, which arises from a protrusion of the embryonic brain,

and whose internal membrane is transformed into the remaining layers of the retina. At a later period the rods and cones are formed from the internal membrane of the ocular vesicle, and project into the pigment layer. Hence the well-known very intimate connection between the two layers.

The pigment cells are uniform six-sided mosaic pieces united so as to form a membrane, in which the individual cells are isolable. The outer portion of each cell, which borders on the choroid, contains little or no pigment, and generally incloses the round nucleus, also in many animals (the Frog) intensely yellow fat-globules. The inner division of the cell contains the characteristic granular coloring matter, and is prolonged in the form of many very perishable processes between the outer segments of the rods and cones, thus forming for the latter pigmented sheaths. These sheath-like processes of the pigment cells are resolved into numberless fine threads, which are often entirely colorless, and not unlike a forest of cilia. They extend in Man at least as far as the division between outer and inner segment, and in many animals almost to the limitans externa. They enclose tightly the rods and cones, but dissolve shortly after death, in consequence of which the union between pigment layer and rods is no longer firm.

After the hardening of the perfectly fresh retina in perosmic acid, the outer segments, even in Man, adhere so closely to the pigment cells that they break off at the point of union with the inner segments, or transversely in their substance, sooner than separate from the cells.

The intensity of the pigment varies, being least in blond individuals and greatest in the negro. Behind the macula lutea the color of the pigment cells is always somewhat darker than in the rest of the retina. The retina of the Albino, and such portions of the retina of the Mammalian as contain a strongly reflecting tapetum, are entirely or almost destitute of pigment. The hair-like ciliated processes, however, which surround the rods like so many sheaths, are well developed even in these colorless cells.*

The pigment granules themselves, which generally appear † to be elliptical and rod-like rather than round, are, according to statements by A. Frisch, small crystals which, in the fresh state and with high powers, present to view sharp angles and corners.‡ These crystals are placed with their long diameters perpendicular to the surface of the retina, and therefore appear rod-like in form when viewed from this direction. Rosow and Frisch found the longest ones to be 4–5 μ in length.

The pathological pigmentation of the retina, accompanied with loss of vision and final blindness, which is known among ophthalmologists by the name *retinitis pigmentosa*, is especially worthy of notice. In this typical form of pigmented degeneration we probably have to do with a degeneration of the pigmented epithelium, at the same time with a degeneration of the rods and cones, and a final atrophy of the nervous elements of the retina. The granular pigment, set free by the deterioration of the pigmented epithelium, passes into the other layers of the retina. This is, of course, only possible after a preceding destruction of certain portions of the rod- and cone-layer and the limitans externa, as well as of the layer of external granules. Arrived in the deeper layers of the retina the granular pigment follows the adventitia of the blood-vessels, or, as is probable, the perivascular lymphatic sheaths. Here it spreads about or deposits itself in more distant localities.

Inasmuch as this condition is either congenital or generally developed in early youth, or hereditary, and especially remarked in the offspring of blood relations (which is well known to be the occasion of congenital malformations), everything

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* M. Schultze, *A. f. m. A.*, Bd. ii., Taf. xiv. fig. 9, *b*.

† Rosow in Graefe's *Archiv*, Bd. ix. 3, p. 65.

‡ "Gestalten des Choroidealpigmentes," *Sitzungsber. d. Acad. zu Wien*, 1869, Juliheft.

combines to mark it, or the disposition to it, as an imperfect development of the outer membrane of the primitive ocular vesicle, which (see development of the retina) is transformed into the pigment epithelium of the retina. It is evident from the intimate relations existing between the pigment cells and the rods and cones, that any morbid process in the former must call for sympathy in the latter, and that thus passing toward the centre the other retinal layers will be affected. Accurate anatomical examinations of this degenerative process, which has been well studied with the ophthalmoscope, are at present only few in number.*

Besides this form of pigmentation, which is essentially fatal to the vision, there appears to be also a more harmless form. This consists in the development of stellated pigment cells (pigmented cells of the connective tissue), in the supporting tissue, and in the adventitia of the vessels, such as often exists in animals—for instance, as observed by me in the Ruminants.

3. The Supporting Connective Substance of the Retina.

Nearly all the layers of the retina are traversed by a tissue which in many places occupies a considerable space by the side of the nerve-tissue: this is the *supporting connective substance.* It is continuous with the connective substance of the optic nerve,† and presents itself in the retina as a framework of a peculiar character, varying in accordance with the different nervous elements which it surrounds in the various layers. This connective substance is nearly related in its structure with that of the brain and spinal cord, and, like that, has received from Virchow the name neuroglia. We describe it as *spongy connective substance*, and distinguish in it the two *limiting membranes*, limitans interna and externa; the radiating fibres as *radial supporting fibres*, in opposition to the radial nerve fibres, and the coarser and finer *networks* which unite the supporting fibres, and which from their similarity to the tissue of a sponge have given a name to the entire system. The membrana limitans interna (limitans hyaloidea of Henle) lies in apposition with the surface of the vitreous body, and often closely attached to it; the limitans externa separates the layer of outer granules from the rods and cones; and stretched out between these two stand in great numbers the radial supporting fibres, like columns extending from floor to ceiling.

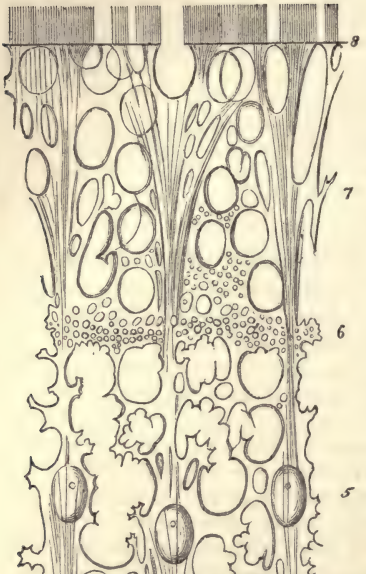
The radial fibres, however, represent but a portion of the connective substance of the retina, since in all the layers they communicate by lateral processes and branches with the spongy tissue lying between them; and from this they are distinguishable only by their greater resistance, which renders it possible to isolate them while the fine spongy network is either destroyed or torn. Thus larger or smaller shreds of the spongy tissue, or at least of the lateral processes, always remain adherent to the radial fibres, and give to them, when isolated, their characteristic rough contour. This network, like that of a sponge, consists not only of fibres but also of membranous sheets, which form sockets and sheaths for the nervous elements, and vary in thickness according to the different layers of the retina, containing large interstices for the reception of the ganglion cells, smaller ones for the internal granules, and the finest for the nerve fibres of the two molecular layers.‡ In the last-mentioned layers the radial fibres are often entirely

* Donders in Graefe's *Archiv*, Bd. iii., p. 139. Schweigger-Seidel, *idem*, Bd. v. 1, p. 96. Leber, *idem*, Bd. xv., 1869, 3, p. 1. An excellent ophthalmoscopic drawing in Liebreich's *Atlas*, Taf. vi. fig. 1. Ivanoff observed a deposit of pigment along the radial fibres (Graefe's *Archiv*, Bd. xi. 1, p. 153).

† Compare Klebs, Virchow's *Archiv*, Bd. xix. p. 321.

‡ In answer to opposing views, especially with regard to the structure of the spongy tissue of the molecular layers (comp. Henle and Merkel in *Zeitschr. f. rat. Med.*, Bd. xxxiv. 1869, p. 51), I could only repeat what I said in my "Untersuchungen über den Bau der Nasenschleimhaut," Halle, 1862, p. 29. I willingly admit that our methods and lens-systems are still too imperfect for the resolution of the mole

Fig. 326.



lost in the spongy tissue, so tha many of them, which may be followe from the limitans interna throug various layers, terminate* in the ex ternal molecular layer, for instance and therefore never reach the layer o external granules. On the other han many of the radial fibres which ma be traced † through the external layer disappear in the network of the in ternal molecular layer, and finall there are radial supporting fibre which reach neither of the two limit ing membranes.

The radial fibres are most constan in the layer of inner granules. I this locality also they generally con tain in their substance homogeneou oval nuclei with distinct nucleoli; o granular protoplasm about the nu cleus no trace is to be seen. These nucleated spaces in the radial sup porting fibres represent the above mentioned second form of inner gran ules. The supporting fibres travers very regularly the layer of opticu fibres, to take part in the formation of the limitans interna. Here th radial fibres stand for the most par in rows corresponding to the arrange ment of the nerve fibres and thei disposition in bundles.‡ They the pass into flattened conical expansions either directly or after previous sub division, like roots from the trunk o a tree, reuniting in several such ter minal expansions,§ all of which finall join to form ‖ a smooth membrane o the surface of the vitreous body namely, the membrana limitans in terna. In many places the membra nous union of the radial fibres is want ing, in which case the interval

Fig. 326. Diagrammatic representation of the connective substance of the retina corresponding to its arrangement in the vicinity of the ora serrata. 1, Limitans in terna; 3, region of the ganglion cells; 4, internal molecular layer; 5, layer of interna granules; 6, external molecular layer; 7, layer of ext. granules; 8, limitans externa beyond which project the fibrils which surround the bases of the rods and cones. × 800

cular substance of the cortex of the brain; but with the observance of every caution and the use of the best immersion lenses, the spongy substance of the retina, even in the molecular layers, is clearly to be recognized as a network.

* M. Schultze, *A. f. m. A.*, Taf. xiv. fig. 6, 8*b*, 8*c*, 10*b*.

† *Idem*, Taf. xi. fig. 13.

‡ Kölliker, *Gewebelehre*, Aufl. 5, p. 680, fig. 488.

§ M. Schultze, *De ret. st. pen.*, fig. 3.

‖ Schelske in Virchow's *Archiv*, Bd. xxviii. p. 482.

between the terminal expansions are filled with a fine fibrous network, and the course of the limitans is interrupted after the manner of filigree-work. Such a picture is presented in surface-views of this membrane in the Rabbit. At the macula lutea, where the opticus fibres do not exist as a distinct layer, and the ganglion cells are situated at the inner surface of the retina, the union of the thicker radial fibres at the limitans interna does not take place. At this particularly delicate portion of the retina, the radial fibres themselves are very scarce. The limitans interna, however, is by no means wanting at this point; on the contrary, it exists as a separable membrane, and is very resistant. As in the other portions of the retina, it appears to be a denser membranous portion of the connective-tissue framework; but it may be separated from the subjacent spongy substance which surrounds the ganglion cells more easily, on account of the greater difference in consistency. The limitans interna is at the macula also plainly rough on its external surface, from the numberless remains of detached fibres, thus betraying its union with the subjacent connective substance. These shreds, however, present an appearance quite different from the arrangement in rows, such as is displayed by the ends of the radial fibres in the more peripheral portions of the retina.

In regard to the membrana limitans interna there prevail certain differences of opinion, which, as I believe, depend upon the varying thickness and consistency of this membrane in different parts of the human retina, and in the retinæ of different animals, and also upon its frequent attachment to the vitreous body. Kölliker* calls attention to the great weakness and perishability of the radial fibres in comparison with the durability of the limitans as being an argument against a relationship between the two, and therefore regards the limitans interna as an independent formation to be reckoned among the vitreous membranes. On the other hand it may be mentioned, that even the vitreous membranes, like the elastica anterior of the cornea, or the inner vitreous membrane of the choroid, are attached to the subjacent tissue and arise with or from it, but nevertheless possess essential differences in their behavior toward solvent reagents. I am unable to find a membrana limitans interna different from that described above; and while I place particular stress on its intimate relations with the reticular framework or spongy connective substance, I fully recognize the separability of the limitans, and the difference in consistency between it and its subjacent tissue, especially at the yellow spot. Henle also considers the limitans interna to be an independent membrane, to whose outer surface the radial fibres are applied † through the medium of their terminal expansions. He calls it, however, limitans hyaloidea, in order to indicate that the special membrane of the vitreous described by many authors is identical with the limitans. The conditions of hypertrophy of the connective substance with atrophy of the nervous elements of the retina are very instructive in displaying the connection between the radial fibres and the limitans interna, as in a case described by Iwanoff,‡ where the hypertrophy of the radial fibres caused circumscribed protuberances reaching into the vitreous.

The limitans externa is not to be considered as an isolable membrane. It consists, exactly like the interna, of a membranous expansion of the radial fibres. Where these do not exist as isolable fibres in the layer of external granules, it is derived from the connective substance surrounding the external granules and their nerve fibres. This connective substance is nowhere

* *Gewebelehre*, 5 Aufl. p. 681.

† *Eingeweidelehre*, p. 658.

‡ Graefe's *Archiv*, Bd. xi. Abth. 1, p. 141, Taf. iii. and iv.

absent,* not even at the yellow spot, where it was unrecognized by the side of the long cone-fibres until Merkel pointed it out† in the form of delicate sheaths surrounding these fibres.

Where, as in Birds, the passage of the radial fibres from the inner to the outer granule-layer is easy to observe, these fibres are seen to divide and form membranous capsules about the external granules and their nervous fibres. If, after moderate hardening of a small piece of retina, the granules, and with them the rods and cones, are separated by agitating the preparation, the tissue of the framework alone remains, and presents a system of sheaths, which can be in some degree understood only by the use of very high magnifying powers. The sheaths themselves show a fine parallel striation, the indication of a fibrillar composition, and although contributing to the formation of the membrana limitans externa, they do not terminate there. For beyond this point project a countless number of fine rigid fibrils (fig. 326, 8) which are arranged in circles, and form the fibrillar framework out of which the cones fall as described above. It appears exactly as if these fibrillæ were continuous with the fibrous sheaths which surround the external granules.‡ What I formerly (*A. f. m. A.*, Bd. ii. Taf. xi. fig. 13) pictured as continuations of the connective-tissue sheaths of the external granule-layer in the Chicken, were evidently fragments of these fibrillar frameworks: these are described by W. Krause under the name of "needles," § and are considered by him as constant elements of the layer of rods and cones. In this connection should be mentioned Iwanoff's drawing of a Human retina, macerated by suppurative inflammation (Graefe's *Archiv*, Bd. xv. 2, Taf. ii. fig. 2), in which the nervous elements were almost entirely destroyed, and only the connective framework remained.

These fibrillar frameworks, which may be isolated in the above-mentioned way, appear to exist in all vertebrate animals as well as in man. How far they are identical with those which are continued over the surface of the outer segments, must be determined by future researches.‖

Besides the nuclei occurring in the radial fibres within the inner granule-layer, nuclei are also to be found in the connective-tissue framework of other layers, although for the most part in small numbers, for instance in the molecular layers.¶ These increase in importance in such pathological processes as go hand in hand with a proliferation of the cells of the connective substance. Although the statements with regard to the proliferation of these cells by division must be accepted with caution, still it may be considered as well established, that under certain circumstances a fine or coarsely granular protoplasm collects about the pale, oval nuclei of the connective substance, and that the number of the latter may become very much greater than in the normal state. The fatty metamorphosis of the retina, moreover, does not restrict itself to the vicinity of the nuclei of the connective substance, but may, as in Morbus Brightii, for example, appear in the form of fine rows of granules, throughout the whole length of the radial fibres, especially in the inner retinal layers, so that one might suppose these fibres to be hollow. In the layer of outer granules, also, I have observed cells which have undergone fatty degeneration, and which from the nature of their nuclei I have been obliged to consider as elements of the connective substance: so that however crowded the nervous cells may be in the layer of external granules, we cannot deny that nuclei of the connective substance may also be present even in the normal state. This is important in its bearing on the first devel-

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* W. Krause's *Widerspruch*, *Membr. fenestr.*, p. 19.

† *Macula lutea*, &c., p. 7.

‡ Compare the drawing, *A. f. m. A.*, Bd. v. Taf. xxii. fig. 4.

§ *Membr. fenestr.*, p. 6, Taf. i. figs. 5 and 7.

‖ In a treatise which appeared in *Archiv f. mikr. Anat.*, Bd. vii. p. 81, E. Landolt expresses the opinion, based upon examinations of the retinæ of Amphibia, that the outer segments of the rods and cones are enclosed in sheaths derived from the connective-tissue framework.

¶ Compare, among others, Nagel in Graefe's *Archiv*, Bd. vi., p. 218.

opment of certain retinal tumors, which received from Virchow the name Gliomata,* indicating that an essential element of them corresponded with the spongy connective substance (neuroglia), and of which it has been affirmed that they may take their origin also from the layer of outer granules.†

We are indebted to H. Müller for information regarding certain smooth, stellate, and anastomosing cells, which are to be found in the Perch and Bull Head (Ascerina cornua), situated ‡ in a double row just interior to the external molecular layer, and which certainly are not ganglion cells. Similar cells have been found in many other animals, although not so easily isolable, and present in their highest development a distinct layer, lying just within the external molecular layer, to which I have given the name "stratum intergranulosum fenestratum." § The substance of this nucleated and anastomosing layer, which presents the appearance of a membrane perforated with a saddler's punch, often has the structure of a reticular (Plagistomen) or fibrillated connective substance (Perca ‖), and, as I have shown, often connects directly with the radial connective fibres. In the Perca Fluviatalis I find this fenestrated intergranular layer to be formed of three distinct layers. The middle is occupied by the flat stellated cells, which anastomose freely, and whose processes are as extensive as the cells themselves, so that this layer resembles rather a network of broad nucleated fibres. These are bounded on one side by a plexus of thin fibres similar to the elastic fibres, which ramify and interlace in such a manner as to form a single stratum of loose areolar tissue. On the other side lies what appears to be a thin sheet of finely granular substance of great delicacy, interspersed with round nuclei and circular holes.

W. Krause has lately described ¶ the external molecular layer in Man and the lower animals as composed of a layer of flat cells with considerable lateral expansion. These cells, which anastomose through their processes so as to form a fenestrated membrane, are also said to be continuous with the rods and cones, since the terminal expansions of the rod- and cone-fibres connect with the substance of the cells or their processes. On the other hand, the radial fibres also which commence at the limitans interna, terminate in this fenestrated membrane and never reach the limitans externa. The interstices, however, of the membrana fenestrata are occupied by peculiar inner granules, which, according to Krause, are the terminal cells of the opticus fibres; with these the rods and cones cannot be continuous, connecting as they do, by means of their fibres, with the fenestrated membrane which appertains to the connective substance. With these views I cannot reconcile the results of my own rerearches.

Finally the blood-vessels of the retina must be reckoned as a part of its connective substance. These, in Man, extend through all the inner layers as far as the external molecular layer, in all parts of the retina except at the fovea centralis. The connection of the external walls of the vessels with the reticular connective substance takes place in a similar manner as in the lymph- and lymphoid-glands. Probably there exist here, as His ** suspected, perivascular lymph-spaces. The course of the vessels will be described in another place.

4. Macula Lutea and Fovea Centralis.

The elements of the retina thus far described suffer an essential change in their form and arrangement at the point where in Man and Apes the yellow spot and central fossa are situated. Not far from the prolongation of the optical axis, and a little to one side of the nerve-entrance, an intense yellow coloring matter is deposited between the elements of the various layers, with the exception of the rods and cones and external granules.

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* *Vorlesungen über Geschwülste*, Bd. ii. p. 158.

† Compare Iwanoff in Graefe's *Archiv*, Bd. xv. 2, p. 84. Iwanoff here evidently goes too far, when he affirms that glioma cannot take its origin in the layer of external granules, since neuroglia, or spongy connective substance, is doubtless present in this layer, as I have demonstrated in *De ret. struct. pen.* 1859.

‡ *Zeitschr. f. w. Z.* Bd. viii. p. 17.

§ *De ret. str. pen.* p. 13, fig. 5, *f*, fig. 6.

‖ M. Schultze, *A. f. m. A.*, Bd. ii. p. 269.

¶ *Die Membrana fenestrata der Retina.* Leipzig, 1868, p. 7–19.

** *Verhandl. d. Nat. Ges. zu Basel*, Bd. iv. 2, p. 256.

The centre of the yellow spot is excavated on its anterior surface, or the surface towards the vitreous, so as to form the fovea centralis. The coloring matter, which at this point is most intense, fades gradually away at the borders of the yellow spot. It does not possess a granular structure, but is completely hyaline, and therefore interferes with the transparency of the retina at this place only in so far as it absorbs a considerable portion of the violet and blue rays before they reach the cone-layer.* With the help of Browning's spectral apparatus I have very distinctly recognized under the microscope a shortening of the violet end of the spectrum, but I have not been able to perceive special absorption striæ. According to Huschke † the intensity of the color of the yellow spot varies, and is found to be lighter in blue-eyed persons than in persons with brown eyes.

The retina at the yellow spot, with the exception of course of the fovea centralis, is thicker than in its vicinity, but is also softer and more disposed to post-mortem changes. Probably the fact that very shortly after death this portion of the retina wrinkles up so as to form the so-called plica centralis, may be explained by its disposition to swell by imbibition. It is well known that the thin centre of the yellow spot is easily torn through, and then appears as a deficiency in its substance (foramen centrale). The fragile and transitory nature of the substance of the yellow spot is explained by the circumstance that the more delicate nervous elements here greatly outnumber the elements of the connective substance, which in other portions of the retina occupy a much more considerable space. For the nervous elements are crowded together at the macula lutea in a manner corresponding with its importance as the most sensitive portion of the retina. The layer of the ganglion cells seems to be the one which thus increases most in thickness; also the inner division of the layer of external granules, which Henle calls the external fibrous layer. On the other hand a continuous layer of nerve fibres beneath the limitans interna does not exist. In the percipient layer the rods diminish in number even at the periphery of the macula, and finally disappear altogether, their place being taken by the cones. The cones, however, which stand closely packed together, gradually diminish in thickness as they approach the fovea centralis, until at this point they are no thicker than the rods. As a consequence of this a much larger number of cones are to be found at the fovea than within an equal area in other parts of the retina. The thickness of the cone-fibres, however, which traverse the layer of external granules, is but little less at the fovea centralis than at the peripheral portions of the retina. The thin cones of the fovea therefore, like the thicker ones of the periphery, are continuous with a like number of primitive nerve-fibrils.

The arrangement of the cones of the yellow spot is wonderfully regular. They stand in curved lines ‡ which converge towards the centre of the yellow spot, so as to form a design similar to that seen on the back of many watches. This arrangement, prophesied by Hensen § on physiological grounds, is developed with complete regularity so long as the cones diminish in diameter in passing from the periphery of the macula to the edge of the fovea. A more uncertain circular arrangement takes place at the fovea itself, where in a circle of about 0.2 mm. in diameter all the cones are of equal thickness.

* According to Preyer (Pflüger's *Archiv*, Bd. i. p. 299), the first suggestions relative to this subject were made by Maxwell. Compare also M. Schultze, *Ueber den gelben Fleck der Retina*, Bonn, 1866.

† Eingeweidelehre in Sömmering's *Anatomie*, p. 727.

‡ M. Schultze, *A. f. m. A.*, Bd. ii. Taf. xii.

§ Virchow's *Archiv*, Bd. xxxv. p. 403.

As the thickness of the cones diminishes in the approach to the fovea, their length increases. Their external segments, which in the more peripheral parts of the retina are hidden between the rods, become at the yellow spot as long as the external segments of the rods, gradually pushing the latter aside and finally surpassing them in length; this is especially the case if at the fovea the other retinal layers recede somewhat toward the vitreous in order to make room for the elongated cones.* In one such case I found the longest cone to be over 100 μ in length. H. Müller and Hulke also found the cones of the fovea to be longer than those of the other portions of the macula.† The thinnest cones of the fovea average at the base 3 μ in diameter. These are distributed in a circular area of nearly 200 μ in diameter, which corresponds to the diameter of the fovea centralis, if we estimate this according to the space occupied by the smallest percipient elements. In this space I have counted in several diameters, in perfectly fresh Human retina, fifteen cones all equally thick. According to this reckoning each cone would have been about 4 μ in diameter. But we must deduct the narrow intervals which exist between the cones. In hardened preparations the measurements of isolated cones are often under 3 μ; Henle found them to be only 2 μ in alcoholic preparations; Welcker, to whom we are indebted for exact measurements of the perfectly fresh retina of an executed criminal, gave the thickness of the cones at the fovea as between 3.1 and 3.6 μ; averaging, therefore, 3.3 μ.‡ The long conical outer segments diminish in size towards the choroid to 1 μ and less. These are surrounded by the sheaths of the cells of the pigment layer, which at the macula lutea are generally darker than in the vicinity, and project as far as the unpigmented external portions of these cells. Hence one may see in the perfectly fresh Human macula, covered by the unchanged pigment cells, the natural ends of the cones like light spots, surrounded with dark coloring matter, as I have observed it in animals, especially in Birds, and as I have represented by a diagrammatic drawing in an earlier work.§

In regard to the size of the external granules and thickness of the cone-fibres, no important difference is to be remarked between this portion of the macula lutea and the more peripheral portions. But the course of the cone-fibres presents essential differences. As has been known since Bergmann's first observations on this subject, the fibres of the external granule-layer, or rather its inner division which contains no cells but only free fibres, here deviate from the radial to take a diagonal course. This change in arrangement commences even beyond the limits of the yellow spot, and becomes more and more marked as we approach the fovea, and the affected layer increases in thickness; at some points the fibres run even parallel to the retinal surface. The fibres of the rods and cones, and finally the cone-fibres alone, bend in lines, which if continued backwards would unite in the fovea or in a prolongation of the optical axis passing through the fovea; thus they do not, like the more peripheral fibres of the layer of external granules, reach the external molecular layer by the shortest possible way. As a consequence of the necessary gradual lengthening of the cone-fibres, there exists in a certain area about the fovea a layer of horizontal cone-fibres, whose beginnings and ends are indeed radial, but which in a

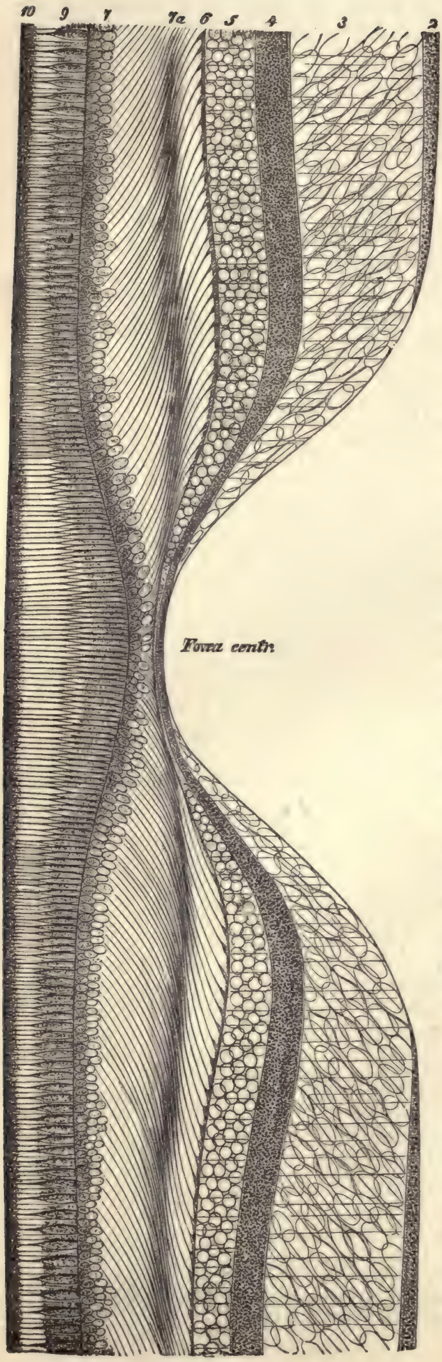
* M. Schultze, *A. f. m. A.*, Bd. ii. p. 227, Taf. xiii. fig. 1.

† Hulke, *Philos. Transact.*, 1857, p. 110.

‡ *Zeitschr. für rat. Medicin*, Bd. xx. 1863, p. 176. Other measurements may be compared: M. Schultze, in Reichert and Du Bois-Reymond's *Archiv*, 1861, p. 784, and H. Müller in *d. Würzb. nat. Zeitschr.*, Bd. ii. 1861, p. 219.

§ *A. f. m. A.*, Bd. ii. Taf. xii. fig. 1.

Fig. 327.



certain plane spread out like radii from the central fovea.* This arrangement finds its explanation in the very existence of the fovea. Here all the layers of the retina, excepting those of the cones and external granules, are reduced to a minimum. The cone-fibres of this region, in order to form their connections, must radiate in all directions; they must find outside of the fovea the inner granules, internal molecular substance, and ganglion cells which appertain to them. But here come masses of new cone-fibres from the uninterrupted cone-layer, seeking also to establish their communications. And although the layer of ganglion cells is considerably thickened at the macula lutea, this is not the case with the layer of inner granules. The fibres therefore crowd away from the yellow spot until, arrived at a point beyond its limits, they reassume the simple radial course, which is the rule in the other portions of the Human retina as well as in the retinæ of the lower animals, where no fovea centralis exists. The diagonal course of the fibres may also extend to the nerve fibres of the layer of inner granules, as was observed by Hulke. In sections through the macula lutea and fovea centralis I found a diagonal course of the rod- and cone-fibres existing in a space 2 mm. wide in the horizontal meridian on each side of the fovea; in the

Fig. 327. Diagrammatic section through the macula lutea and fovea centralis of the Human retina, ×110; 2, opticus fibres; 3, ganglion cells; 4, internal molecular layer; 5, layer of internal granules; 6, external molecular layer; 7 *a*, external fibrous layer; 7, layer of external granules; 9, rods and cones; 10, pigment layer.

* Merkel, l. c. fig. xi., Taf. 1.

vertical meridian, however, only 1.5 mm. wide. According to the statements of Rud. Schirmer, the ophthalmoscopic picture of the macula in the healthy eye always appears as an oblique oval, so that its horizontal diameter is to the vertical as 4 : 3.*

The ganglion cells of the yellow spot are for the most part bipolar, as has been remarked by various observers, and recently by Merkel.

The connective substance at the macula is, as has already been observed, peculiarly delicate, and dispenses with the thicker radial fibres. The membrana limitans interna, on the other hand, becomes a boundary of considerable solidity. It attains, according to Merkel, a thickness of 3 μ, but at the fovea centralis becomes markedly thinner again. It is very easily detached from the delicate spongy connective substance which lies between the ganglion cells (compare above page 835).

Among Mammalia a macula lutea with a fovea centralis occurs only in the Apes, and here the structure corresponds essentially with that in Man.† Remak and H. Müller‡ have made some observations with regard to an area centralis, similar to the yellow spot in structure, existing in several of the Mammalia, but accurate information on this point is wanting. H. Müller § discovered in the retina of certain Birds not only one but two fossæ, quite distant from one another, but failed to make any observations with regard to the percipient elements found at these points. According to my researches, the percipient elements of the two central fossæ in the retina of the Falcon are cones; these cones are thinner than those in the vicinity, and are provided only with yellow globules, and not with red ones also, as are the cones of the other portions of the Bird's retina; no rods are to be found between the cones.‖ The retina of the Chameleon possesses a well-developed fovea, on the minute structure of which we have exact reports from H. Müller¶ and Hulke.** In the percipient layer of the entire retina of the Chameleon cones only are found, as appears to be the rule with Reptiles. These are, however, at the fovea, only a fifth as large as in the peripheral regions, and at the same time much longer, so that the line of the limitans externa here recedes from the choroid, just as I have represented it in Man. To these cones are attached cone-fibres running obliquely as in Man. But while in Man the connective substance of the external granule- and cone-fibre layer follows these fibres, H. Müller observes in the Chameleon a peculiar kind of radial fibres which cross the cone-fibres at an acute angle. The fineness of certain cones from the Chameleon, judging from what I have seen in preserved eyes of this animal, surpasses anything yet known in the way of cones from other Vertebrata.

A fovea appears to exist, though less marked, in other Lizards also, and in Snakes and Turtles, according to statements by Knox and Hulke.†† In the Amphibia and Fishes, on the other hand, nothing like a macula lutea or fovea centralis is known.

When I called attention to the fact that the yellow screen, which at the macula lies in front of the percipient elements, must have an essential influence over the quantity of violet and blue which we perceive in the spectrum in the act of direct vision, it wanted but a step to intimate that an increase in the intensity of the yellow pigment must cause yellow vision or violet blindness (compare my above-mentioned treatise on "the yellow spot of the retina, its influence on normal vision and on color-blindness"). When also, in this connection, I spoke of the santonin intoxication I overlooked what I here expressly mention, namely, that in it objects will be seen yellow not only in direct but also in indirect vision. I retract, therefore, my former opinion, which indeed I have long since ceased to hold. We see, however, through still another yellow screen, namely, the finely meshed network of capillary vessels, which throughout the whole retina lies in front of the percipient elements, between the limitans interna and the external molecular layer. The number of spectral rays which a single

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* Graefe, *Archiv*, Bd. x. 1, p. 150.

† M. Schultze, *Sitzungsber. d. niederrhein. Ges. zu Bonn*, Juli, 1861.

‡ *Würzb. naturw. Zeitschr.*, Bd. ii. 1861, p. 140.

§ Idem, und *über das Auge des Chamäleon*, p. 11.

‖ *A. f. m. A.*, Bd. ii. p. 206.

¶ *Würzb. nat. Zeitschr.*, Bd. iii. 1862, p. 10.

** *Journal of Anatomy and Physiology*, 1866, No. I. p. 104.

†† L. c. p. 103 and 104.

layer of blood-globules, arranged on edge like rows of coin, may absorb, is very considerable, as is taught by the examination with the spectral apparatus of Browning. The hæmoglobin striæ are visible, and at the violet end of the spectrum a considerable portion of the rays are lost. When the layers of blood-globules are thicker, as in the larger retinal vessels, the absorbing power will of course be much greater. Notwithstanding the fact that in this screen of blood-globules there are many intervals, through which we see, and of whose existence we are unconscious owing to the continual movements of the eye, still the network of blood-vessels, especially if projected upon a single plane from the various layers of the retina, is too dense not to be taken into consideration. Changes in the blood, which affect its power of absorbing certain rays of light, must therefore also occasion abnormal perception of color (compare here my communications to Preyer in Pflüger's *Archiv*, Bd. i., p. 305).

5. Ora Serrata and Pars Ciliaris.

In contrast with the macula lutea, the region of the ora serrata in the Human retina is characterized by a gradual disappearance of the nervous elements at the same time with an increase in the development of the connective substance. The radial supporting fibres, and the spongy network which unites them, represent the mass of tissue at the ora serrata; these also, although in an altered form, appear to constitute the prolongation of the retina over the ciliary processes, which portion of the retina, however, takes no part in the act of vision.

H. Müller made such thorough researches * of this region, that but little remains to be added by later investigators. His account is essentially as follows:—

"In the vicinity of the ora serrata all the layers of the retina are so reduced that its thickness is not more than 0.12–0.14 mm. Nerve and ganglion cells are very scarce, so that they are to be found singly between the ends of the radial fibres; the molecular layer presents a more perpendicularly striated appearance, owing to the increased number of radial fibres, so that finally its inner border is erased; the layer of internal granules consists of only two to three scattered rows; and frequently in its place only nuclei seem to be deposited in the fibrous mass, which stretches through the thin intergranular layer to the external granules. The rods and cones are distinct, although somewhat shorter than elsewhere. Very shortly before the extreme thinning of the retina its layers lose their specific characteristics, even more than before, and are transformed into an indistinctly fibrous mass, whose fibres run in a perpendicular direction, and in which numerous round or oval nuclei are deposited. The rod-layer alone is excepted in this general commingling, since it retains, even to the last, its existence as a separate layer; its elements diminish in size somewhat suddenly, and then disappear altogether; and at the same time the other layers of the retina are reduced to a single row of cells, which represents the pars ciliaris, and is an immediate continuation of the retina itself. These cells resemble in general the cylindrical epithelia, but in different animals (H. Müller examined this region in Oxen, Swine, Rabbits, Pigeons, and Chickens) are of different height (in the Rabbit 0.25 mm.)."

H. Müller considers these cells as a continuation of the general connective framework of the retina, "to which must probably be reckoned the inner ends of the radial fibres, perhaps also that portion of the internal granules which in most animals distinctly corresponds to the various nucleated radial fibres." "The form also of the cells in question is, in a certain degree, such that they could not well be taken for epithelial cells.

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* *Z. f. w. Z.*, Bd. viii. p. 91.

Thus, when isolated, their ends are often not rounded, but furnished with several indentations and short processes, which occur also on the sides, so that they may well be considered as belonging to the group of connective substances; whereas the round cell-forms which occur elsewhere present no such tendency."

Kölliker* corroborates these views, in so far that he professes to have observed a gradual transition of the shortened radial fibres into the cells of the pars ciliaris. He also assumes here a prolongation of the limitans interna. We miss, however, a more accurate description of the isolated cells, whose forms, as stated by H. Müller, may be very manifold, by reason of processes and indentations, and of which Klebs,† depending upon his own researches, affirms that they may be directly continuous with the fibres of the zonula. Two regions are to be distinguished here, namely, the smooth posterior region, and the anterior region, bordered by the ciliary processes. These were designated by Schwalbe‡ as the zone of the orbiculus ciliaris, and the zone of the ciliary processes. Schwalbe was able to isolate the limitans interna in both these regions; but when the vitreous body is separated from the ciliary processes, the limitans remains attached to the zonula zinnii. This attachment occurs at the places corresponding to the valleys between the processes; and these places are also covered with the cells of the pars ciliaris and pigment, thus giving rise to the well-known appearance of the zonula. Schwalbe, however, does not, like Kölliker, admit that the limitans interna arises from the cells of the pars ciliaris, but distinguishes it (together with certain external reticular processes, seen also by Merkel,§ which extend between the cells, and represent the radial supporting fibres) as a continuation of the connective substance of the retina.‖ Thus the transition of the radial fibres of the retina into the cells of the pars ciliaris, which Kölliker considers as certain, is again brought into question.¶

According to my researches made upon fresh Human eyes, which had been preserved for twenty-four hours or somewhat longer in varying solutions of perosmic acid, the cells of the pars ciliaris present a great diversity in appearance. In general they are elongated and prismatic, resembling tall, cylindrical epithelium. At their outer ends they are smoothly truncate, and lie each upon a pigment-cell; at their inner ends they may either increase or diminish in size, and adhere closely to the surface of the vitreous body, which at this point is distinctly fibrous (zonula Zinnii). Many of the cells end here distinctly, after the manner of the radial fibres of the retina, in conical expansions, or divided into branches, each of which again terminates with a truncate extremity, like a column standing upon its base. Others, interposed between these, reach the surface of the corpus vitreum only by a pointed end, or terminate in a fine fibre, so as to give the appearance of being continuous with the fibres of the zonula. Such a transition, however, I have not in reality seen. The entire surface of the cells of the pars ciliaris is frequently provided with serrations and roughnesses, by which the neighboring cells hold fast to one another. The substance of the cells is not homogeneous, but marked with exceedingly fine striations, in the longitudinal direction; it cannot, however, be resolved

* *Gewebelehre*, Aufl. 5, p. 685.
† Virchow's *Archiv*, 1861, Bd. xxi. p. 187.
‡ *A. f. m. A.*, Bd. vi. p. 326.
§ *Die Zonula ziliaris* Leipzig, 1870. Taf. 1, Fig. 9.
‖ *Idem.*, p. 303.
¶ Compare also the notice by Manfredi: "Sulla struttura dela parte cigliare della Retina" (*Gaz. Med. Ital. Lombard*, Ser. vi. Tom. iii. 1870).

into fibrillæ. The nucleus is oval, hyaline, very pale, resembling the nuclei of the radial supporting fibres, and lies sometimes near one extremity, sometimes near the other. In the substance of the cells it is not uncommon to find a small quantity of blackish-brown granular pigment, which is denser at the outer end of the cells, so that it seems doubtful whether another special pigment-cell lies upon the pigment-layer of the retina, or whether the pigment-cell itself is provided with fibrous prolongations. Taking all things into consideration, the opinion that the cells of the pars ciliaris correspond with the radial supporting fibres seems to me to be the correct one. They agree in the nature of their substance, which in both cases is finely striated, as if having a fibrillar structure; in the form and refractive quality of their nuclei; in their reaction to perosmic acid, in which both take a light-brown color, while the neighboring vitreous, after a time, becomes bluish-black, and finally in the rough serrated surface, and the manner of termination at the vitreous body.

It has been often affirmed that the cones of the human retina, as compared with the rods, diminish in number continuously from the macula lutea to the ora serrata. This is not the case, as I have indeed heretofore stated.* From a certain circle surrounding the yellow spot to the ora serrata the distribution of the rods and cones remains the same, so that always three to four rods occupy the shortest space between two cones. At the ora serrata the number of rods suddenly diminishes, and empty spaces occur between the cones, which seem to become more numerous. The latter, when seen from the surface, resemble irregularly distorted circles, lose their brilliancy, and finally disappear apparently in the tissue of the pars ciliaris. The length of the cones and rods in the region of the ora serrata is less than in the fundus or equator of the eye, as in fact H. Müller observed.† Merkel remarked similar appearances in Man, Cattle, Chickens, and the Pike.

A very remarkable deviation from the normal condition, which accompanies atrophy of the nervous tissues at the ora serrata, is represented by the condition which Iwanoff and I have called œdema of the retina. Iwanoff has lately devoted an exhaustive essay to this subject.‡ According to Merkel § and Iwanoff this change occurs by preference in elderly people, and therefore is to be considered as a senile metamorphosis.‖ It is characterized by the formation of spaces filled with serous fluid, which by uniting may expand the retina considerably, and lead to an atrophy of the nervous tissue at the affected spots; the radial fibres, however, are crowded together in columnar bundles, which remain stretched between the two limitantes, or between the limitans interna and the external molecular layer. This appearance was excellently described by H. Müller,¶ who thought it should be considered as a post-mortem change; Blessig first made drawings of it,** and Henle described it as being of frequent occurrence.†† In transverse sections of such œdematous portions of retina one may see empty spaces within the limits of the granule-layers, or, when the degeneration is far advanced,

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* *A. f. m. A.*, Bd. ii. p. 225, Taf. xii. figs. 3–4.

† Compare M. Schultze, *A. f. m. A.*, Bd. v. Taf. xxii. Fig. 5, vom vorderen Rande; Fig. 14, aus der Gegend des Aéquators; fig. 11, vom gelben Fleck des Menschen.

‡ Graefe, *Archiv*, 1869, Bd. xv. 2, p. 88.

§ *Macula lutea*, etc., p. 17.

‖ Iwanoff, who examined a large number of cases with reference to this point, saw this œdema only 6 times out of 50 in eyes of adults between 20 and 40 years of age; on the other hand 26 times out of 48 in eyes of persons 50–80 years old.

¶ *Z. f. w. Z.*, Bd. viii. p. 7.

** *De retinæ textura*, Dorpat, 1855, fig. 3, p. 47.

†† *Eingeweidelehre*, p. 669.

stretching from the limitans interna to the externa. These spaces are bounded by columns of condensed radial fibres, which contain many nuclei, and which in the vicinity of the limiting membranes communicate with one another in the form of arches. This form of degeneration does not occur exclusively at the ora serrata. I myself observed one case where a portion of the retina not far from the equatorial region was swollen so as to form a prominent tumor of the size of a pea; a cross section of this tumor showed it to be a highly developed œdema limited to this spot. The retina at this point was 1 mm. in thickness. The rods and cones remain apparently unchanged in the low degrees of œdema, but are generally wanting where the retina is much swollen.* Merkel observed this œdematous swelling also in the eyes of old dogs.

6. Development of the Retina.

For the development of the retina the embryonal brain puts forth a vesicular protrusion, the primitive ocular vesicle, which after its formation is changed by the simultaneous development of the lens into a sac very soon having a double membrane. This happens in the Chick by the end of the second day of incubation. The two folds of the primitive retina, which arises from the ocular vesicle, are at first equal in thickness, but soon the anterior fold, which borders on the vitreous, becomes considerably thicker, while the posterior fold remains the same.† The former on the fifth day of incubation consists of very numerous small fusiform cells, which stand perpendicular to the surface; the latter is formed of a single layer of short prismatic cells in which dark pigment is deposited. Remak thought this might be considered as the foundation of the retina, and with it the choroid. But it has been demonstrated by Kölliker ‡ and more recent observers § that the development of the pigmented connective tissue and the blood-vessels of the choroid advances independently of the pigmented layer of the primitive ocular vesicle. The posterior fold of the latter is destined exclusively to the pigmented epithelium of the retina, while the anterior forms the other layers of this membrane. The rods and cones make their appearance last. Before their development the embryonal retina is sharply separated from the pigmented epithelium by the limitans externa, which at this stage of development is much more distinct than the limitans interna. In its position the externa, since it is turned toward the cavity of the primitive ocular vesicle, corresponds to the inner surface of the cerebral ventricle; which in the embryo of this age I find to be covered by just such a distinct limiting membrane. It consists of the conical expansion of fibrils and fusiform cells, arranged perpendicularly to the surface, and whose ends fall in the same plane and unite in the form of a membrane. The appearance is precisely the same in the retina and in the ventricles of the brain. At this time there is nothing to be seen of an epithelial covering in either place.

While now in the Chick, from the seventh to the tenth day of incubation,

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* Compare Iwanoff, l. c. Taf. iv. und v. figs. 11 und 12.

† Compare Remak, *Entwickel. d. Wirbelthiere*, p. 35, Taf. v. fig. 60. Hensen, Virchow's *Archiv*, Bd. xxx. p. 181, and my full description of the development of the retina in the Chicken, *Archiv f. m. A.*, Bd. ii., p. 239, Taf. viii.

‡ *Entwickelungsgeschichte*, 1861, p. 288, für Säugethiere.

§ Babuchin, *Würzb. nat. Zeitschr.*, Bd. iv. 1863, p. 71, für Säugethiere, Huhn und Frosch. M. Schultze, l. c. für das Hühnchen und für Säugethiere. Schenck, *Sitzungsb. d. Acad. zu Wien*, 1867, Aprilheft, betrifft Fische. Comp. also Hensen, *A. f. m. A.*, Bd. ii. p. 421.

a very distinct stratification takes place throughont the previously homogeneous (anterior) retina, consisting in the division into an internal fibrous layer, two molecular layers, and a differentiation in size of the various layers of granules and ganglion-cells, the beginnings of the rods and cones push out beyond the posterior surface of the limitans externa in the form of semicircular protuberances, small in size and homogeneous in character. As these increase in length and thickness the inner segment is first formed, and somewhat later the outer segment. At the same time they insert themselves into the posterior retinal fold, which goes to form the pigment-sheaths. On the eighteenth day of incubation, small oil globules, at first red and afterwards yellow, are to be found within the cones, so that the retina of the chick as it emerges from the egg is already provided with fully-developed percipient elements, which increase afterwards in size, but probably not in number. It is worthy of remark that in the chicken the rods and cones appear from the beginning as distinctive structures, and that the cones, which at first are inferior to the rods in diameter, become considerably thicker immediately after hatching, and ultimately with their colored globules occupy a relatively much larger space than at an earlier period. We are indebted to Babuchin, in his researches on the retina of the tadpole,* for information concerning the relation of the developing rods and cones to the external granules. The relative size of the elements reveals clearly the fact that the rods and cones owe their existence to an outgrowth of the substance of the external granules. Although the rods and cones in the mature frog differ very much in appearance, this difference is, according to Babuchin, less marked during the earlier stages of development.

These observations on the development of the rods and cones from the anterior fold of the primitive ocular vesicle are corroborated by Schenk's remarks about fish. The process may be ranked with the so-called cuticular formations, in so far as it consists in a unilateral proliferation from the cell of a substance not protoplasm, as is certainly the case with the outer segments and the refractive bodies of the inner segments.†

As in the Chicken the rods and cones, although not so thick as in the mature animal, are already developed before the moment of hatching, so is it in Man at the time of birth, as well as in many of the Mammalia, for instance the ruminants. Rods and cones in the newly-born child as in the newly-born calf are well developed, and divided into inner and outer segment, although much thinner and shorter than in the adult. The case is different with the young of the Rabbit and the Cat, which are born blind. Here the percipient elements are only developed after birth.‡ Whether at the time of birth the limitans externa is quite smooth, or the first indications of rods and cones have pushed beyond the limitans in the form of roundish protuberances, certain it is that the complete formation of the rod-like elements follows some days after, and progresses as in the Chicken, in such a manner that first the inner segment and later the outer segment is formed. The first recognizable laminæ of the latter make their appearance on the fifth or sixth day after birth. On the ninth day, or at the time when the eyelids

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* L. c. p. 77.

† Hensen advocated for some time the opinion that the rods, or at least the outer portions of their substance, were developed simultaneously with the pigment from the external fold of the primitive ocular vesicle (Virchow, *Archiv*, Bd. xxx. p. 181, and *A. f. m. A.*, Bd. ii. p. 421), but has lately changed his views on this subject (*idem*, Bd. iv. p. 349).

‡ M. Schultze, *A. f. m. A.*, Bd. iii.; *Idem*, Bd. iii. p. 373; Steinlin, *Anat. d. Retina*, St. Gallen, p. 39.

are opened, the length of the outer segment in the Kitten is scarcely 4 μ, while in the full-grown animal they are more than 17 μ long. The conditions are similar in the Rabbit.* Here the thickness of the laminæ does not increase, but only their number.† At what time before birth the development of the rods and cones from the layer of external granules begins in Man is not precisely known. In an embryo of twenty-four weeks, which came to my hands perfectly fresh, I found the membrana limitans externa still quite smooth. Ritter thinks that he has seen well-developed rods in even younger embryos.‡

In the earliest period of its formation the retina reaches forward beyond the border of the lens. By a difference in development of its various parts are formed the true retina, the pars ciliaris, and finally the pigment covering the posterior surface of the iris, which latter is covered only by a rudiment of the tissue arising from the inner fold of the primitive ocular vesicle, or by the so-called prolongation of the limitans interna. Since during the development of the retina the position of the embryonal ocular fissure is indicated by an unpigmented stripe running from behind forwards throughout the entire extent of the retina,§ the foundation is thus laid for that arrest in development consisting in a lack of pigment (coloboma) which frequently exists at this place, and which may involve the pigment of the iris as well as that on the anterior surface of the choroid. The coloboma is, as Schöler‖ has already rightly stated, originally an arrest in development of the retina and not of the choroid.¶ To what degree the tissue of the last-mentioned membrane and of the iris, leaving out of the question the pigmented epithelium, take part in the frequently occurring colobomata is to be determined from the numerous and exact ophthalmoscopic examinations of this anomaly. Here doubtless some unknown relation exists between the development of the pigmented epithelium from the outer fold of the primitive ocular vesicle and the development of the choroidal tissue.

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* M. Schultze, l. c. Bd. iii. p. 375.

† W. Krause's *Widerspruch*, *Membr. fenestr.* p. 33. I take this opportunity of mentioning the fact that reliable information concerning the development of the rods and cones can only be obtained by examining the edges of absolutely fresh retinæ prepared in humor aqueus or iodized serum; all my statements are based upon examinations made in this way. W. Krause puts the eyes of young rabbits in bichromate of potash, and finds that the existence of rods and cones may be demonstrated without the slightest difficulty at a time when I miss them in a fresh state.

‡ Graefe, *Archiv*, Bd. x. 1, p. 75; 2, p. 142. *Die Structur der Retina, etc.* p. 22 u. 52.

§ Compare *A. f. m. A.*, Bd. ii. Taf. viii. fig. 7.

‖ *De oculi evolutione.* Dis. inaug. Mitau, 1849.

¶ The situation of the fovea centralis forbids the supposition that it is a remnant of the fœtal ocular fissure, as recently stated by Hensen (*A. f. m. A.*, Bd. iv. p. 350). On the contrary the pecten of the Bird, and what corresponds to it in reptiles and fishes, occupies this region, consisting, as it does, of an outgrowth of the choroid into the fissure itself (Schenck, *Wiener Sitzungsber.* 1867).

II. TUNICA VASCULOSA.

By Prof. A. IWANOFF.

The tunica vasculosa or tunica uvea forms the internal lining of the sclerotica, being situated between the latter and the retina. At a point 1 mm. from the margin of the cornea, it bends abruptly towards the axis of the eye, and applies itself in the form of a vertical septum to the anterior surface of the lens, thus forming the posterior wall of the anterior chamber.

The posterior portion of the tunica vasculosa, which lies in contact with the sclerotic, is called the vascular membrane or choroid; the anterior portion, which during life is visible behind the transparent cornea, and which is provided with a central aperture, the pupil, has received the name iris.

Both these membranes bear the name "tunica vasculosa" in common, for the reason that both are extremely vascular, and the vessels of both stand in intimate relation with one another. The second name common to the choroid and iris, "tunica uvea," was given on account of a distant resemblance to the skin of a dark-colored grape, in which the hole for the stem is represented by the pupil (Brücke*). Many anatomists also still apply the name uvea particularly to the layer of pigment which covers the posterior surface of the iris.

1. The *choroid* presents a thin (0.08–0.16 mm. in thickness) vascular tunic, which at two points is united to the sclerotic more firmly than elsewhere: posteriorly, at the entrance of the optic nerve, where its inner layers form a ring, surrounding the optic nerve, and from which thin filaments penetrate the nerve itself;† and anteriorly, at the junction of the sclerotic with the cornea (annular tendon of the ciliary muscle). In addition to this these two membranes are bound together by arteries and nerves which perforate the sclerotic to enter the choroid, and by veins taking the opposite course.

The external surface of the choroid, or the one turned toward the sclerotic, is brown in color and fibrous; anteriorly, at the junction of the choroid and sclerotic, may be seen a gray circular thickening, 3–4 mm. in breadth, which encircles the anterior portion of the vascular membrane; this is the ciliary muscle.

The internal surface is turned toward the retina, and as far as to the ora serrata very loosely attached to it. The attachment, however, is such that in the great majority of cases the outer layer of the retina (namely, the pigmented, epithelial layer) remains adherent to the choroid, which gave rise to the fact that this layer has hitherto been considered as belonging to the vascular tunic of the eye. In front of the ora serrata these membranes are more intimately united, since from this point the pigment layer increases in importance as a medium of connection between the ciliary portion of retina

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* *Anatom. Beschreibung des menschlichen Augapfels*, 1847, p. 2.

† Anat. Beiträge zur Ophthalmologie, *Arch. f. Ophth.*, Bd. ii. *Abth.* 2, p. 24.

and the choroid, in consequence of which also the separation of the retina from the choroid at this point cannot always be effected, and then only partially. If the pigment is removed, the inner surface of the choroid, as as far as the ora serrata, appears completely smooth and gray in color; behind the ora serrata its surface is rough; in front may be seen a row of elevations arranged in the meridional direction, and separated by deep interspaces—the so-called ciliary processes, processus ciliares.

The ciliary processes, 70–80 in number, have the appearance of a regularly folded ruffle, and since their prominences become more and more elevated towards the front, they finally reach as far as the ciliary margin of the iris. Their entire inner surface, with their folds, are covered even to their anterior limit, with a thick layer of pigment, and with the cells of the ciliary portion of the retina (pars ciliaris retinæ).

The anterior portion of the choroid, commencing at the ora serrata and including the ciliary processes and the ciliary muscle, is called corpus ciliare.

The anterior portion of the choroid has for a long time possessed a particular designation. Thus Vesal called it tunica ciliaris, and later anatomists distinguished in this tunica ciliaris a pars plicata and non-plicata. Fallopius was the first who named this portion of the choroid corpus ciliare. Henle gave the name corpus ciliare only to the most anterior part of the choroid, including the ciliary processes and ciliary muscle; the zone between ora serrata and corpus ciliare he called orbiculus ciliaris, without stating that between the corpus ciliare and orbiculus ciliaris there was any distinct boundary line. Luschka describes under the name corona ciliaris that portion of the vascular membrane which is attached to the zonula Zinnii, and which spreads itself from the ora serrata to beyond the margin of the lens; the ciliary muscle he calls annulus ciliaris. We consider it advisable, for the sake of the more easy comprehension of the ordinary terminology, to hold exclusively to some one name, even if it should not give expression to all the anatomical peculiarities of this region of the choroid. We have chosen the name corpus ciliare, not because we considered it to be absolutely the best, but because it has been most generally adopted; for this reason Kölliker also in his text-book uses the name corpus ciliare, likewise H. Müller in all his treatises on the eye.

The *vessels* constitute the principal portion of the choroid; hence to it was attributed even in former times a great influence over the nutrition of the eye. This vascularity is without doubt the occasion of the exceedingly important part which the choroid takes in the various intra-ocular pathological processes.

Another constituent part of this membrane, of importance in the functions of the eye, is formed by the *smooth muscular fibres*, of which the largest part are deposited in the corpus ciliare, but which also exist in the posterior regions of the choroid.

Finally, this vascular membrane is richly provided with *nerves*.

All these elements are bound together by a *stroma*, which in the choroid is characterized by a great number of stellated pigment-cells.

The choroid is usually divided into the five following layers:—the pigment-layer, the vitreous membrane, the membrana chorio-capillaris, the layer of larger arteries and veins, and finally the membrana supra-chorioidea. The pigment layer, by reason of its development from the external lamella of the secondary ocular vesicle, must be reckoned with the retina, so that for the true choroid only four layers remain. Since the division of choroid into these four layers is not founded upon any histological or topographical grounds, we shall not adhere to it in our description.

1. The vitreous membrane, vitreous lamella, lamina vitrea (F. Arnold*),

* *Anatomie*, ii. p. 1020.

elastic layer (Kölliker*), or basal membrane (Henle†) was first described by Bruch‡ and called by him membrana pigmenti. It makes its appearance in the posterior portions of the choroid as a very thin (0.0006–0.0008 mm.), apparently structureless, or faintly fibrous membrane, which without the use of artificial means remains indissolubly attached to the choroidal stroma. The surface which is turned toward the pigmented epithelium is perfectly smooth as far as the ora serrata. Treatment with potash and sulphuric acid causes folds to appear in it, since these reagents act differently upon the vitreous membrane and the outer layers of the choroid to which it is attached. Since by long-continued action of these reagents a part of the stroma which adheres to the vitreous membrane is gradually destroyed, it often separates itself after treatment with concentrated alkalies and acids in the form of isolated shreds. If the choroid is immersed for a considerable time in a 10 per cent. solution of common salt, the fibrous structure of the vitreous membrane becomes more apparent; but even after this treatment no nuclei are to be seen in it. The nuclei in the vitreous membrane, described by Bruch and Henle, doubtless belong to the capillaries.

In the anterior portion of the choroid, in the corpus ciliare, the characteristics of the vitreous membrane change in a great degree. Here it is paler, thicker, and is more susceptible to the action of alkalies and acids. It loses its smoothness, and presents upon its surface microscopical depressions and elevations, which form the so-called reticulum of the ciliary body (H. Müller§). This reticulum is formed of small anastomosing elevations, which enclose after the manner of a network the excavations in which pigment is deposited. The meshes of this reticulum are smaller in proportion as they are distant from the ora serrata. The reticulated structure of the vitreous membrane may be followed as far as the iris.

2. The vessels of the choroid, as already mentioned, form two layers: the chorio-capillaris, known also under the name of membrana Ruyschiana (this layer does not extend beyond the ora serrata), and the layer formed by the coarser arterial and venous trunks, which has also been called tunica vasculosa Halleri. The ramifications of these vessels will be specially discussed elsewhere; here there is only room for a few remarks upon certain peculiarities of their structure.

The capillaries are so intimately united with the vitreous membrane by means of a very thin connective stroma, that separation can be effected only by the use of reagents which dissolve the stroma.

The walls of the capillaries are identical in structure with the capillaries of other regions of the human organism; contrary to Henle's opinion, their walls contain nuclei, and not only in young individuals, as stated by H. Müller, but also in persons advanced in years. In aged people the nuclei are simply somewhat atrophied, and become flatter, while simultaneously the walls of the vessels are thickened, thus rendering them more difficult of observation.

One may often see in the eyes of apparently healthy persons elongated cells deposited along the walls of the capillaries, and connecting with them by very thin processes, visible only by the use of high powers. These cells, however, become exceedingly conspicuous in inflammation of the choroid. In such cases the processes extend also into the spaces between the capillaries.

* *Handbuch der Gewebelehre*, 1867, p. 661.
† *Handbuch der systematischen Anatomie des Menschen*, 1866, II. Bd. p. 620.
‡ *Körniges Pigment*, 1844.
§ *Arch. f. Ophth.* Bd. ii, 2. *Anatomische Beiträge zur Ophthalmologie.*

The arteriæ ciliares breves are distinguished by a great development of their circular muscular fibres. Besides this, on both sides of them are arranged longitudinal bundles of smooth muscular fibres (H. Müller*), whose number is in different individuals very variable. Also the size of the muscular bundle is not alike on both sides of the same vessel. The smooth muscles accompany the branches of the short ciliary arteries only in the posterior part of the choroid, and become more scarce in proportion as we advance in the direction of the ora serrata.

Muscular fibres, arranged in thin bundles, are also to be found detached and scattered throughout the choroidal stroma between the vessels.

3. The principal mass of the smooth muscular fibres of the choroid is situated in the foremost region of this membrane; this is the ciliary muscle (tensor choroideæ, Brücke).

The ciliary muscle (Fig. 328) presents itself in the shape of a triangular prism, which is bent upon itself so as to form a ring, and whose acute angle is directed backwards. Its situation is in the anterior and external portion of the ciliary body. The ciliary muscle is separated from the sclerotic by

Fig. 328.

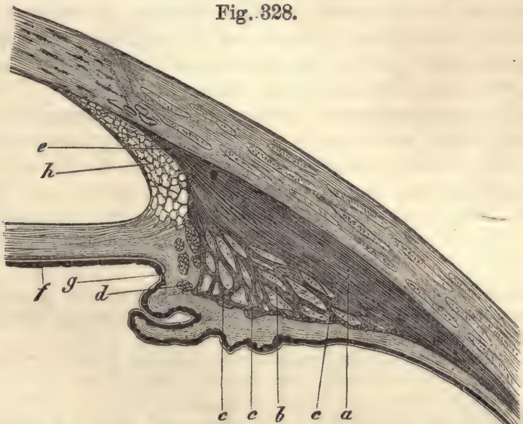

Fig. 328. Section through the ciliary region of the Human eye. *a*, meridional bundle of the musc. ciliaris; *b*, deeper radiating bundle; *c c c*, circular plexus of muscular bundles; *d*, annular muscle of Müller; *f*, muscular layer on posterior surface of the iris; *g*, muscular plexus at ciliary margin of the iris; *e*, annular tendon of musc. ciliaris; *h*, ligamentum pectinatum.

a thin lamella, the lamina fusca, and from the pigment covering the inner surface of the ciliary processes by connective tissue. In meridional sections the ciliary muscle presents the form of a right-angled triangle, whose shortest side is directed forwards, and forms with the external side a right angle. The thickness of the muscle equals 0.8 mm.

The greater part of the muscle is made up of meridional (Fig. 328, *a*) bundles, which as a compact mass form the thick outer layer, and the largest third of the muscle.

The deeper bundles (*b*), which, like those just mentioned, take their origin at the anterior external angle of the muscle, then diverge in a radial direction toward the inner side of the triangle. In this course the radiating bundles anastomose frequently with one another. After they have reached

* *Verhandl. d. physical-medicin. Gesellchaft in Würzburg*, Bd. x., Abth. 2, 3, p. 179.

the inner side, they change their direction for a circular one, and thus form a dense circular plexus (*c*) along the internal surface of the entire muscle.

Moreover, the anterior side, and in part the anterior and internal angle of the ciliary muscle are occupied by moderately thick bundles of circular fibres, the so-called *annular muscle of Müller* (*d*). Its posterior bundles alone are formed by those longitudinal fibres which have changed their direction; the anterior bundles represent an entirely independent muscle.

All the meridional and radial bundles arise from the anterior and external angle of the muscle. Their prolongations, consisting of compact, flattened connective tissue, form the annular tendon of this muscle (*e*). It passes forwards along the inner side of the canal of Schlemm, and finally is lost in the tissue of the cornea.

The meridinal portion of the muscle, which lies immediately against the sclerotic, consists anteriorly of regularly arranged laminæ which lie parallel to one another. This regularity, however, disappears as we pass further backwards, and 3 mm. from the origin of the muscle the bundles, as they separate from one another and anastomose, form a row of loops with the convexities looking backwards, in which a portion of the muscle terminates. The other portion of the meridional fibres retains its original direction, and may be followed in the form of the finest fasciculi even to a distance of 5–6 mm. from the beginning of the muscle, where they finally disappear among the pigment cells of the stroma of the ciliary body.

These bundles may be traced further only on the temporal and nasal side of the choroid; here, united into two fasciculi, they are prolonged on each side of the long ciliary arteries. In many eyes H. Müller observed that these bundles, after they had accompanied the ciliary artery throughout its course in the choroid, were also to be traced for some distance in the scleral canal.

The ciliary muscle was first discovered by Brücke* in the year 1846, and shortly after, independently of him, by Todd and Bowman. Brücke, Todd, and Bowman, exactly speaking, described only its meridional bundles.

The complete description of this muscle was given by H. Müller † in the year 1857. In this treatise he described for the first time the circular bundles, which run parallel to the corneal margin, forming the anterior and inner portion of the ciliary muscle—the compressor lentis, as he called it. Simultaneously with him Arlt ‡ also discovered the circular fibres of this muscle, which he regarded only as processes of the radial fibres.

Finally F. E. Schultze, in the year 1867, with the help of the chloride of palladium, found the circular plexus, which is spread over the entire inner surface of this muscle.

The size of the muscle, its texture, the relative development of its meridional and circular fibres, are subject to great individual variations. These variations are in relation with the length of the axis of the eye, on which depends the refractive condition of the eye—that is, its far- or near-sightedness.

In the hypermetropic eye,§ the axis of which is generally shorter than normal, the anterior portion of the muscle—that is, the annular muscle of Müller—is excessively developed; as a consequence of this, the muscle is pushed considerably forwards in the direction of the anterior chamber, and the entire muscle is smaller.

In the myopic eye, the axis of which is considerably longer than normal, the anterior circular bundles of the muscle are very poorly developed; the muscle itself consists principally of meridional and radial bundles, hence in this case the anterior por-

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* Müller's *Archiv*, 1846.

† *Archiv für Ophth.*, Bd. iii.

‡ *Archiv für mikr. Anat.*, Bd. iii., p. 477.

§ *Arch. für Ophth.*, Bd. xv. Abth. 3, p. 284. *Beitr. zur Anatomie des Ciliarmuskels*, von A. Iwanoff.

tion of the muscle is crowded considerably backwards, and the entire muscle appears longer.

In the domestic animals the ciliary muscle consists wholly of longitudinal fibres; in Swine alone circular bundles are found in the posterior portion of the muscle (A. Iwanoff and A. Rollett *).

Fig. 329.

Fig. 329. Section through the ciliary region of a hypermetropic eye.

Fig. 330.

Fig. 330. Section through the ciliary region of a myopic eye.

4. The nerves of the choroid (nervi ciliares) are branches of the third and fifth pairs, and of the sympatheticus. The long ciliary nerves (nervi ciliares longi), two and rarely three in number, arise from the nasal branch of the ophthalmic nerve (ramus naso-ciliaris trigemini); the short ciliary nerves (nervi ciliares breves), 14–18 in number, proceed from the ciliary ganglion. Both perforate the sclerotic not far from the optic nerve, and continue their course on the external surface of the choroid. After having given off a considerable number of branches to the posterior portion of the choroid, they

* *Arch. f. Ophth.*, Bd. xv. Abth. i.

advance to the ciliary muscle, where they bifurcate, and are resolved into a thick terminal plexus. In the angle formed by the first bifurcation of these nerves H. Müller* found ganglion-cells 0.0016–0.025 mm. in diameter, with two to three nuclei. Also in the deeper layers of this plexus, in the interior of the muscle, are to be found nodular swellings very similar to bipolar cells.

In the posterior part of the choroid the arrangement of the nervous network † is such that the ciliary nerves, immediately after their passage from the sclerotica and throughout their course to the ciliary muscle, distribute lateral branches, which consist partly of dark-bordered and partly of pale nerve fibres. These lateral branches, after repeated divisions and anastomoses, form a plexus lying between the vessels and the sclerotic. From this network twigs may be traced to the arteries, where they terminate apparently in the smooth muscular fibres. In this nervous network also ganglion-cells are to be found, which are situated at the nodal points. Ganglia also occur even in the small branches of the ciliary nerves.

It is worthy of notice that the development of the posterior nervous network, as well as the number of ganglion-cells which are to be found in it, is subject to important individual variations; and quite as remarkable is the fact, that these variations stand in striking relation with the development of the smooth muscular fibres in the posterior portion of the choroid.

5. The stroma of the choroid is formed of a dense network of interlaced fibres, in the interspaces of which, especially of the external layers, a great number of stellate pigment-cells are embedded.

The fibres of this network, while they anastomose with one another, take for the most part a course parallel to the surface of the sclera, and give off but few processes to the adjacent layers; thus is presented an appearance as if the fibres were woven into several distinct layers, of which one generally remains adherent to the sclerotic (lamina fusca), while another, thicker, goes with the choroid. The latter resolves itself into several superimposed laminæ, which, beginning at the posterior portion of the ciliary body, extend to the entrance of the optic nerve (membrana suprachoroidea).

The fibrillar stroma which occupies the interspaces between the blood-vessels is in connection with the membrana suprachoroidea.

The choroidal stroma is very rich in cells. The most characteristic are the stellate pigment-cells, whose form is somewhat different in the superficial and deeper layers of the choroid. The cells of the superficial layers display a stellate form, with short, broad, and flat processes; the dark-brown pigment does not invade the nuclei, which are therefore always distinctly visible. The stellate cells, which occupy the deeper layers and fill up the spaces between the vessels, are somewhat thicker, and provided with long thin processes, which form frequent anastomoses with the processes of the neighboring cells, thus constructing a dense network. These cells are generally darker than the more superficial ones.

Unpigmented cells, also of the most various forms, are to be found in the choroid; of these the rounded cells, which in size and form present a strong resemblance to the white blood-corpuscles or lymph cells,‡ deserve a special mention. They are met with in all the layers of the choroid, but especially in the deepest layer between the capillaries. These cells have the power, like the white blood-corpuscles, of changing their form and place. Their number is subject to great variation, according to the age and state of health

* *Verhandl. d. phys.-med. Gesellschaft in Würzburg*, Bd. x. p. 108.
† L. c., Bd. x. p. 189.
‡ Haase, *Arch. f. Ophth.*, Bd. iv. p. 57.

of the eye. They are very numerous in children; in adults their number is disproportionately small and varies greatly. They make their appearance in great quantities in every intra-ocular pathological condition.

The external surface of the supra-choroidea, according to recent researches by Schwalbe, is covered with endothelium.

The question as to the nature of the tissue of which the choroid is composed, cannot be decided alone by histological, but also by histogenetic researches. The lack of the latter gave rise to the fact that at one time the choroidal stroma was arbitrarily reckoned as connective tissue, and at another time as elastic tissue.

II. In the *Iris* we distinguish the pupillary border (margo pupillaris), which limits its central aperture, the pupil; and the ciliary border (margo ciliaris), which completes the union with the ciliary body and the cornea; furthermore, an anterior and a posterior surface.

On the anterior surface of the iris is to be remarked a jagged line, by which this surface is divided into two zones. The inner, pupillary zone, about 1 mm. in breadth, is set with fine radiating folds, which are closely laid together; the outer, ciliary zone is a little less than 3 mm. in breadth (the pupil being 4 mm. in diameter, or the average size in the cadaver), and possesses in its external half five to seven concentric folds, which are always distinctly to be seen, but especially when the pupil is dilated.

The anterior surface of the iris is covered with epithelium, which is in fact a continuation of the epithelium of the membrane of Descemet; it differs, however, somewhat from the latter in consisting of smaller cells, which are granular and not so plainly hexagonal, and also not so sharply separated from one another as the epithelial cells of the membrane of Descemet.

The posterior surface of the iris is black in color, owing to the thick layer of pigment which covers it, the so-called uvea. The uvea begins at the edge of the pupil, which in a state of contraction is plainly bordered with it (during the dilatation of the pupil this border disappears first of all), and ends at the ciliary margin, being continuous with the pigment-layer of the ciliary processes. (The boundary-line between the pigment of these two regions is always sharply marked, since the pigment of the ciliary processes is covered by the pars ciliaris retinæ even up to its point of contact with the uvea.)

In a histological point of view the uvea consists of cells whose protoplasma is interspersed with pigment-granules, by which the nucleus is completely hidden from view. Portions of this layer, picked to pieces and examined with the microscope, present masses of the most various dimensions and with rough surfaces, so that it is impossible from these fragments to determine the shape of the cells. The nuclei, when completely free from pigment, are round and faintly granular.

The free surface of the uvea exhibits a series of shallow folds, which take a radial direction, and extend in the form of regular straight lines from the pupillary to the ciliary margin; they are 70–80 in number.

In Man there exists no covering membrane for this pigment-layer. That which was formerly described under the name membrana limitans Pacini (or Jacobi) pigmenti is, according to Kölliker, "the united outer cell-wall of the pigment-cells;" according to Henle it is the margin of the cement-substance which holds together the pigment-granules—an explanation which seems the more probable, since it is impossible to demonstrate a cell-wall in the cells of this layer.

The tissue of the iris, like the tissue of the choroid, consists of vessels, muscles, nerves, and the stroma.

The vessels of the iris are distinguished in general by the unusual thickness of their walls (Arnold), especially the adventitia, which by itself is considerably thicker than all the other tunics. Moreover, the walls of the vessels of the iris display a high development of the muscular elements (Arnold and Hüttenbrenner).

The movements of the iris are accomplished by two muscles; the sphincter, which contracts the pupil, and the dilator, through whose agency the pupil dilates.

The sphincter of the pupil (fig. 331, *a*) occupies the pupillary zone of the iris, and extends from the edge of the pupil outwards for a distance of 0.9–1.3 mm. At the pupillary margin it is thinnest (0.10 mm. in thickness), becomes thicker externally, and at a point not far from its outer border reaches a thickness of 0.25 mm. It lies nearest the posterior surface of the

Fig. 331.

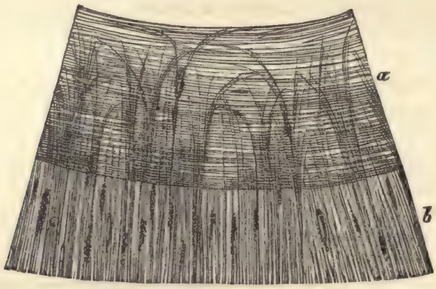

Fig. 331. Segment of the iris, viewed from the surface. *a*, **sphincter;** *b*, **dilator.**

iris, so that it is separated from the uvea only by a thin layer of connective tissue, and some exceedingly delicate muscular bands belonging to the dilator.

The dilator pupillæ (fig. 331, *b*) is developed from the bundles of the sphincter as an uninterrupted continuation of the same. Its beginning is formed by a series of arched interlacing bundles, which lie partly within the sphincter, and partly on its posterior surface between it and the pigment-layer. These isolated bundles, after they have passed the boundary of the sphincter, unite to form a continuous muscular layer, which spreads over the entire posterior surface of the iris (fig. 328, *f*); all its fibres lie regularly parallel to one another, and all are arranged in lines radiating from the pupillary to the ciliary margin.

At a distance of ½ mm. from its point of insertion the muscle divides up into single bundles, which arrange themselves in two layers one above the other (fig. 332, *a*, *a′*). Just at the ciliary margin the fibres of these bundles again change their direction, and bend abruptly around (*b*) to form, by interlacing with one another, a thin muscular plexus (*c*), which surrounds the ciliary margin of the iris in the form of a ring (Fig. 328, *g*).

The literature on the dilator pupillæ leads us unwillingly to the belief, that until the time of Henle the existence of this muscle was presupposed on the ground of absolute physiological necessity, rather than actually demonstrated. Of the fact that the greater number of authors have seen this muscle in the lower animals, there can be no doubt; it is also probable that the observations there made were directly applied to Man, but, owing to the peculiarities presented by the entire human accommodative and muscular apparatus, such a simple transfer to Man of the results obtained in ani-

mals is not practicable. . The peculiarities in the structure of the dilator in Man compelled Henle himself justly to remark, that between the object which he was describing, and that which Brücke and Kölliker called the dilator, there was nothing in common.

Fig. 332.

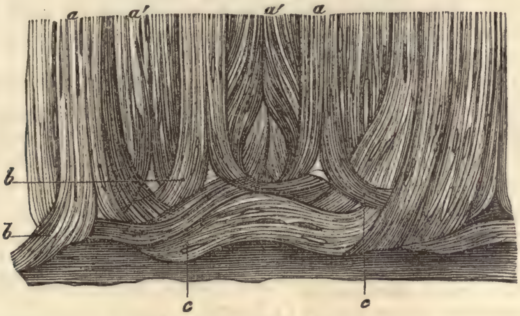

Fig. 332. Arrangement of muscular bundles in the iris. Explanation of letters to be found in the text.

Kölliker * himself does not conceal the fact that his description of the dilator in the Rabbit was borrowed. According to him the dilator consists of isolated thin bundles, which lie between the vessels, and therefore in the substance of the iris. Henle † calls attention to a special layer of fibres which is to be found on the inner surface of the iris, and believes that this homogeneous and uninterrupted, although very thin layer of radiating fibres, which extend from the pupillary to the ciliary margin of the iris, should be looked upon as the muscle whose contraction is followed by dilatation of the pupil.

This declaration gave rise to new researches concerning the dilator. According to Hüttenbrenner ‡ the dilator in the Rabbit exhibits the continuous layer of muscular fibres described by Henle, which lies immediately under the epithelium, which in this animal takes the place of the pigment-layer. This muscle extends to the ciliary margin, and some of its fibres may easily be followed as far as the ligamentum pectinatum. This is obviously not the muscle that Kölliker saw in the Rabbit. In Hüttenbrenner's opinion the dilator in Man also is arranged in the same manner. This author therefore, with the single exception of the prolongation of the muscular fibres into the ligamentum pectinatum, confirms the views of Henle, and not for Man alone, but also with regard to animals.

Merkel § again describes and delineates the dilator more according to Kölliker's definition; he does not speak of a uniform and continuous layer, such as Henle saw, but of isolated bundles, which, however, are situated, as Henle described, just behind the pigment.

Dogiel ‖ describes a muscle, which conforms with the descriptions given by Brücke and Kölliker; it arises at the sphincter on the anterior surface of the iris, and, dividing into separate bundles, takes a course between the vessels from within outwards to be inserted into the ciliary ring.

In consideration of these differences of opinion I called upon Mr. Jeropheef to investigate the dilator in Man. The results of this investigation are imparted above; they agree entirely with the description given by Henle. Mr. Jeropheef, moreover, has succeeded in discovering the circular bundles at the ciliary margin.

The *nerves* of the Human iris, owing to the great difficulties which attend their examination, have been up to the present time very unsatisfactorily

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* *Handbuch der Gewebelehre des Menschen.* 1867, § 667.
† *Handb. d. system. Anat. des Menschen.* Bd. ii, p. 635.
‡ *Sitzungsber. d. k. Acad. d. Wissensch.*, 1 Abth. 1868.
§ *Zeitschr. f. rat. Med.*, xxxi., xxxiv.
‖ *Archiv für mikr. Anat.*, Bd. vi. p. 95.

investigated. The best researches on this subject are by Arnold;* and these in fact relate only to the nerves of the Rabbit.

The nerves of the iris are branches of the ciliary nerves of the choroid. After they arrive at the iris they divide dichotomously in its external zone, form loops, and are finally resolved into a plexus consisting of nerve-trunks of medium size. In this plexus may be remarked an interchange of the fibres of the nerve-trunks, thus calling to mind the arrangement of the fibres in the chiasma nerv. opticorum.

From these points of intersection three kinds of nerve-fibrils take their origin: *a*, pale fibres, in all probability belonging to the sympatheticus, which take their course toward the posterior surface of the iris (consequently toward the dilator), and upon it form an exceedingly fine plexus; *b*, medullated fibres, which advance to the anterior surface, and there are resolved into a compact network of fine fibres; these are the sensitive fibres of the iris; *c*, finally, a third plexus is distributed within the sphincter; its delicate fibres are for the most part motor.

The vessels, muscles, and nerves lie embedded in a *stroma*, which consists mostly of connective-tissue fibrils and cells. The connective tissue accompanies the vessels in the form of thin fibrils; also in the spaces between the vessels fibres are to be found, which generally take a longitudinal direction.

In black eyes the principal part of the stroma consists of stellate pigment-cells, communicating with one another by frequent anastomoses. These cells are most numerous in the more superficial layers of the iris. In addition to these, many round, strongly pigmented cells are found lying free in the stroma of black eyes.

In light eyes stellate unpigmented cells with long, thin processes are to be found, and also a great number of round cells resembling the lymph-cells.

III. THE BLOOD-VESSELS OF THE EYE.

By Th. LEBER.

The blood-vessels of the eyeball form two almost entirely separate systems, the *system of retinal vessels*, and the *system of choroidal or ciliary vessels*, which communicate with one another only by a number of small branches at the entrance of the optic nerve.

The *system of retinal vessels* supplies besides the retina, also a portion of the trunk of the optic nerve; the *system of ciliary vessels*, besides the choroidal tract (choroid, ciliary body, and iris), also the sclerotic, the corneal margin, and that portion of the scleral conjunctiva which is adjacent to the latter.

The remaining portion of the conjunctiva receives special vessels, which arise from those of the eyelid, and form the *system of conjunctival vessels*.

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* *Archiv. für path. Anat. und Physiol.*, Bd. xxvii.: "Ueber die Nerven und das Epithel der Iris."

I.—Vascular System of the Retina.

The vascular system of the retina is derived from the arteria and vena centralis retinæ. The artery is one of the first branches of the ophthalmic, and enters the trunk of the optic nerve diagonally at a distance of 15–20 mm. from the eye; the vein leaves the nerve at a point somewhat nearer. The latter as a rule empties directly into the sinus cavernosus, but generally first undergoes an abundant anastomosis with the ophthalmica sup., into which it sometimes immediately opens; it rarely terminates in the ophthalmica inf.* The central artery and vein of the retina run alongside of one another, and surrounded by a certain amount of connective tissue, in the axis of the opticus, as far as its intraocular end. During this course they distribute to the trunk of the nerve small branches, which take their course in the network of connective tissue surrounding the nerve-bundles.

Besides the branches of the central vessels, the optic nerve receives also numerous twigs from the vessels of the inner sheath, *f* (the true neurolemma of the nerve), and also from those of the outer sheath, *g*, although in less numbers. These vessels are branches of the ophthalmic and its first divisions. The intercranial portion of the optic nerve, the chiasma, and the tractus are supplied by the vessels of the pia mater and the brain, which are distributed to this region of the cranial cavity, and whose ramifications are in communication with the vessels of the intraorbital portion of the nerve.

At its entrance into the eye the optic nerve receives also branches from certain (2–3) of the short ciliary arteries, *k*. These form, in the sclerotic, a complete vascular zone, surrounding the optic-nerve entrance (the zone of Zinn or Haller †), which sends numerous fine twigs into the optic nerve, to anastomose with the branches of the central artery.

There are no veins corresponding to these branches of the ciliary arteries; on the contrary, the finer arteries, veins, and capillaries of the choroid, at the margin of the optic nerve, are directly continuous with the corresponding vessels of the papilla and the internal sheath of the nerve, so that at this place there exists quite an intimate connection between the retinal and ciliary vascular systems, *b*.

No other connection between these two vascular systems exists; at the ora serrata all the retinal vessels terminate in capillary loops, without communicating in any way with the vessels of the choroid.

The central vessels traverse the axis of the optic nerve as far as the surface of the papilla, at which point, or rather just before reaching it, they divide into their principal branches. The division takes place dichotomously, and the vein generally divides somewhat sooner than the artery. The principal branch of the artery as well as of the vein takes its course upwards, the other downwards, soon to divide again into two diverging branches. The veins often accompany, or at least are not far from, the larger branches of the arteries; the latter are finer than the corresponding veins. Moreover, the individual differences presented in the course of the vessels are quite numerous. A large vessel is never seen to take its course directly toward the

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* Walter, *De venis oculi*. Berol., 1778. Sesemann, "die Orbitalvenen des Menschen und ihr Zusammenhang mit den oberflächlichen Venen des Kopfes." Reichert und Du Bois' *Archiv*, 1869, p. 2.

† Illustrations to be found in Jäger, *Ueber die Einstellungen des dioptr. Apparats*, Wien, 1861, Taf. iii. Fig. 34–36; and Th. Leber, "Anat. Unters. über die Blutgefässe des menschl. Auges." *Denkschr. d. Wiener Acad.*, Bd. xxiv. Taf. iv.

temporal region across the macula lutea (or only in very exceptional cases, Mauthner); all the larger vessels pass around the yellow spot in curves to reach the peripheral portions of the retina, and send from all sides only the smaller vessels to the macula; similar small vessels also pass directly

Fig. 333.

Fig. 333. *Diagrammatic representation of the course of the vessels in the eye.* Horizontal section. Veins black. Arteries light. *a*, art. cil. post. br.; *b*, art. cil. post. long.; *cc'*, art. and ven. cil. ant.; *dd'*, art. and ven. conj. post.; *ee'*, art. and ven. centr. ret.; *f*, vessels of the internal, *g*, of the external optic sheath; *h*, ven. vort.; *i*, ven. cil. post. brev.; *k*, branch of art. cil. post. brev. to the opticus; *l*, anastomosis of choroidal vessels with those of the opticus; *m*, chorio-capillaris; *n*, episcleral branches; *o*, art. recurrens chor.; *p*, circ. art. irid. maj. (transverse section); *q*, vessels of the iris; *r*, ciliary process; *s*, branch of ven. vort. from the ciliary muscle; *t*, branch of ant. ciliary vein from the ciliary muscle; *u*, circ. venosus; *v*, plexus of the corneal margin; *w*, art. and ven. conj. ant.

thither from the papilla. These supply the macula, but terminate all together in capillary loops, at the margin of the fovea centralis, so that this latter is entirely without vessels.

The capillary network of the retina is distinguished from that of the choroid by much wider meshes; the capillaries themselves are finer, and possess very thin walls. The ramifications of the vessels of the retina have a great similarity with those of the central organs of the nervous system. According to His, perivascular lymph-spaces, similar to those of the vessels of the brain and spinal cord, are to be found surrounding the vessels of the retina.

The coarser branches of the central vessels all lie in the nerve-fibre-layer of the retina, and the more external or peripheric the layer, the smaller will be the vessels to be found in it. The vessels reach as far as the intergranular layer; the layer of external granules and the rod-layer are, like the fovea centralis, devoid of vessels.

In the fœtus the central artery gives out also the arteria hyaloidea, which passes forwards from the papilla of the optic nerve, through a canal in the vitreous body, to the posterior surface of the lens, and covers it with vessels. This has already completely disappeared at the time of birth, and only in rare cases, and generally in an obliterated condition, is the artery met with in extra-uterine life.

In many animals the retinal vessels are wanting, or are distributed only to a limited portion of the retina.

In Birds, many Amphibia, and Fishes they are altogether absent, but here are generally, though not always, represented by vessels of the hyaloidea, which are spread over the internal surface of the retina (Huschke, Hyrtl, H. Müller). Among Mammalia, the Rabbit has vessels only in that portion of the retina which is distinguished by medullated nerve fibres. In the retina of the Horse only very small vessels are to be found, which resolve themselves into a delicate zone of capillary loops, not more than 3–6 mm. in breadth.* In the Guinea-pig there is to be seen with the ophthalmoscope only an occasional diminutive vessel on the papilla, which cannot be followed into the retina.

II. Ciliary or Choroidal Vascular System.

The entire choroidal tract, the sclerotic with the corneal margin, and the adjacent scleral conjunctiva are supplied by the so-called ciliary vessels. These are as follows:—

a, *Arteries.*

1. The *short posterior ciliary arteries*, art. cil. post. brev. figs. 333 and 334, *a*, 4–6 small twigs, which arise from the ophthalmica or its first branches. They divide, as they follow the trunk of the optic nerve, into a large number of branches, which (about 20 in number) pierce the posterior portion of the sclerotic, and pass from without inwards in a pretty direct course. The most numerous and largest branches enter in the vicinity of the posterior pole of the eye; a smaller number pass to the inside of the insertion, and in the immediate neighborhood of the opticus. These are also generally of less calibre, and some of them give off, at the nerve-entrance, the branches already mentioned above.

2. The *long posterior ciliary arteries*, art. cil. post. long., *b*. Their origin is the same as that of the short ciliary arteries; they perforate, two in number, the sclerotic, somewhat further forward than the latter, in the hor-

* H. Müller, "Notiz über die Netzhautgefässe bei manchen Thieren." *Würzb. naturw. Zeitschr.*, ii. p. 64.

izontal meridian of the eye—one on the medial, the other on the lateral side. Their passage through the sclerotic is very diagonal, so that the artery runs in a scleral canal as much as 4 mm. in length.

3. The *anterior ciliary arteries,* art. cil. ant., *c*, which are not direct branches of the ophthalmica, but arise from the arteries of the four recti

Fig. 334.

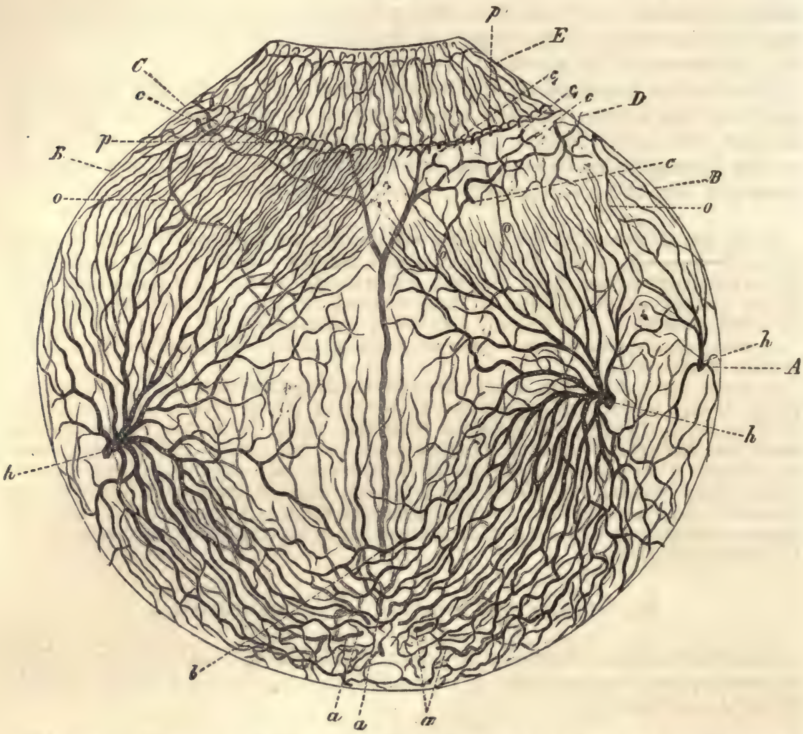

Fig. 334. *Partially diagrammatic representation of the course of the vessels in the choroid.* *A*, choroid; *B*, smooth portion of the ciliary body, orbiculus ciliaris; *C*, ciliary processes (the ciliary muscle removed); *D*, ciliary muscle; *E*, iris; *a*, art. cil. post. brev.; *b*, art. cil. post. long.; *c*, art. cil. ant.; *c'*, ven. cil. ant.; *h*, ven. vort.; *o*, art. recurr. chor.; *p*, circ. art. irid. maj.

muscles of the eye. Generally two arteries arise from each muscle, but only one as a rule from the rectus externus. They pass over to the sclerotic at the insertion of the tendon, take a rather tortuous course towards the cornea, and, after giving off some fine superficial branches, pierce the sclerotic with their perforating branches in an oblique direction, not far from the margin of the cornea.

b, *The veins of the ciliary vascular system* are:—

1. The so-called *venæ vorticosæ*, *h*, generally four in number, which empty either directly into the ophthalmic vein or into the muscular branches. They perforate the sclerotic in the equatorial region in the same slanting manner as the long ciliary arteries. Often one or several of them divide before en-

tering the sclerotic, and thus the number of perforating vessels is increased to six, but seldom surpasses that number. Divisions also occur during the passage through the sclerotic and immediately after, so that, besides the 4–6 larger vessels, a varying number of smaller vessels also enter the choroid.

2. The small *venulæ cil. post. brev.*, fig. 333, *i*, like the arteries of the same name, enter the sclerotic in the neighborhood of the optic nerve, but correspond only to the scleral branches of the artery, and receive no branches from the choroid. They are, therefore, much less numerous, and much smaller than the corresponding arteries.

3. The *venæ cil. ant.* are, like the arteries of the same name, branches of the veins of the recti muscles, but are smaller than the arteries, because the territory supplied by the branches of their perforating twigs is much more limited.

There are no veins corresponding to the course of the arteriæ cil. post. long.

A. The Sclerotica

receives small branches from all the principal vessels which have been described. These are, however, not numerous, and form, especially on the surface, a coarse network, in which generally two veins, one on each side, accompany each artery. The episcleral vessels of the anterior portions of the sclerotic bordering on the cornea have a different arrangement, but these will be described hereafter, in connection with the vessels of the corneal margin and the conjunctiva.

B. The Choroid

is supplied by a great number of vessels, which ramify and interlace in its tissue in the most profuse manner.

This abundant vascular development, which reaches its highest point in the ciliary processes, appears to be intended to secrete the fluid which maintains the intraocular tension, since this would otherwise rapidly diminish by continuous filtration through the walls of the eye. Moreover, the choroidal vessels may, perhaps, be destined to nourish the external unvascular layers of the retina, a supposition which seems the more probable since in many animals, as has been already stated, the entire retina is destitute of vessels, in which case, doubtless, the nutrition must take place through the choroid.

From the above enumeration of the vessels of the ciliary vascular system, it is evident that the arteries and veins of the choroid do not at all correspond. *The choroidal tract, in so far as relates to its arterial supply, may be divided into two rather distinct regions: the first, consisting of the choroid itself*, receives its blood by the *short posterior ciliary arteries; the second, consisting of the ciliary body and iris*, is supplied by the *long posterior* and the *anterior ciliary arteries.* The most anterior portion of the choroid receives also a number of recurrent twigs from the anterior region, and thus is formed a communication between the two arterial regions.

The arrangement of the veins is quite different. *The greater part of the venous blood of the entire choroid* (choroid, ciliary body, and iris) *has a common outlet through the venæ vorticosæ, and only a portion of the blood from the ciliary muscle discharges itself by the small anterior ciliary veins*, so that this anterior outlet is far less important than the other.

1. Arteries of the Choroid.

The branches of the short ciliary arteries lie in the posterior region of the choroid, at first in the most superficial layer of this membrane, surrounded by some loose, and generally darkly pigmented tissue. During the first part of their passage forwards they follow a very tortuous course, and then, always dividing dichotomously, gradually pass into the deeper layers of the choroid. The finest branches are lost in the capillary plexus, which covers the entire internal surface of the choroid, the so-called chorio-capillaris. The branches which pass forwards are distinguished from the veins by their straighter course, while the finer twigs found in the neighborhood of the optic nerve are, like the veins, quite tortuous. This circumstance, and the great number of vessels in this region, account for the fact, that in well-injected preparations we here meet with an almost irresolvable maze of fine vessels.

Besides the branches which are resolved into capillaries, there are no other branches which are directly continuous with the veins, as was formerly supposed.* This opinion was based upon deceptive appearances, which might easily have presented themselves with the use of the old-fashioned opaque injection-substances, but which may be avoided with the use of the transparent coloring fluids.†

The short ciliary arteries are completely lost in the capillary network of the choroid, and give off no branches further forwards to the ciliary body and iris. The former supposition, with regard to the existence of such branches, depended on a confusion with veins passing from the ciliary body to the venæ vorticosæ. On the contrary, the most anterior portion of the choroid receives a number of *recurrent branches*‡ from the long posterior and anterior ciliary arteries. These run backwards in varying number and size, and at wide intervals, between the numerous parallel veins of the orbiculus ciliaris, and supply the foremost regions of the choroid with capillaries, anastomosing in part with the terminal branches of the short posterior ciliary arteries.

The *capillary network* covers continuously the entire inner surface of the choroid, from the optic-nerve entrance to the margin of the orbiculus ciliaris (which corresponds to the ora serrata of the retina), and terminates here with an irregular indentated border. Its meshes are, in the vicinity of the optic nerve, irregularly round and very fine, but become more elongated in proportion to the distance from the nerve; the longitudinal diameter finally becomes 8–10 times as great as the lateral diameter; also the diameter of the capillaries themselves increases at the same time.

In the orbicularis ciliaris there are no true capillaries.

2. Arteries of the Ciliary Body and Iris.

The two long posterior ciliary arteries, after their passage through the sclerotic, run on the external surface of the choroid in a horizontal direction

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* Brücke, *Anatomische Beschreibung des menschlichen Augapfels.* Berlin, 1847, p. 14.

† Th. Leber, "Anat. Unters. über die Blutgefässe des menschl. Auges." *Denkschr. der Akad. zu Wien*, xxiv. Math. natw. Cl. p. 301. Ders., "Unters. über den Verlauf und Zusammenhang der Gefässe im menschl. Auge." *A. für O.*, xi. 1, p. 15.

‡ These recurrent branches were first described and drawn by Haller (*Tab. art. ocul.*, Tab. vi. fig. 4), and by Zinn (*Descr. anat. oc. hum.*, ed. ab H. A. Wrisberg, Goett., 1780, p. 39), but were afterwards forgotten, until I discovered them again (loc. cit., p. 303 u. 306. Taf. ii. 12.)

forwards to the ciliary muscle, without giving off any branches. Here they divide into two branches, which separate obliquely from one another and penetrate the substance of the muscle; arrived at its anterior end, they bend around in a perfectly circular direction, so that both branches of each artery meet each other in the circumference of the eye. The circular plexus of vessels thus formed is completed by branches of the anterior ciliary arteries, which pass directly from the sclerotic to the ciliary muscle. Thus is formed at the anterior border of the muscle a complete arterial circle, the *circulus arteriosus major*, which supplies especially the iris and ciliary processes, while the arteries of the ciliary muscles and the rami recurrantes of the choroid may be derived not only from it, but also directly from the ciliary arteries.

In many animals in whom the ciliary processes are situated farther forward on the posterior surface of the iris, for instance, in the Rabbit, the circulus irid. maj. does not lie in the ciliary muscle, but in the iris, at a short distance from the ciliary margin.

Besides the circulus irid. major, the long and anterior ciliary arteries form, farther back in the ciliary muscle, an incomplete circle of anastomosis.

The *arteries of the ciliary muscle* divide in an arborescent manner, thus following the course of the muscular bundles, and display a rather dense, trellis-like capillary plexus, which differs essentially from the network of the subjacent ciliary processes.

The *arteries of the ciliary processes* are derived from the circulus irid. maj., and must, therefore, like those of the iris, all previously pass through the ciliary muscle. They are small trunks which are quickly resolved into a great multitude of branches, which inosculate freely with one another, and, gradually enlarging, pass over into the commencements of the veins. These capillary veins form by abundant anastomoses a highly developed vascular plexus, which makes up the principal part of the ciliary processes.

The great increase of the surface by numerous larger and smaller elevations and groove-like depressions, the greater width of the capillary veins, the consequent delay in the current of the blood, and the thinness of the vessel-walls, combine to make the ciliary processes the principal secreting organ of the fluids of the eye.

The *arteries of the iris* arise as numerous, somewhat tortuous trunks from the anterior border of the circ. art. major, and divide up dichotomously in the substance of the iris. Their walls are very thick in comparison with their calibre. Their branches are distinguished from the colored tissue of the iris as radiating and plexiform anastomosing lines on its surface; in albinos only the color of the blood shines through the walls. Not far from the pupillary margin the arteries form a second circle of anastomosis, the so-called circulus irid. minor.

The capillary network of the iris is much more widely meshed than that of the choroid; at the pupillary margin the finest arteries terminate in loops and are continuous with the beginnings of the veins. The sphincter pupillæ is traversed by a special, finer capillary plexus.

3. Veins of the Choroid.

The *venæ vorticosæ*, *h*, generally 4–6 larger, and often a varying number of smaller vessels in addition (perhaps ten in all), are distinguished by the spiral course of their branches, which radiate in all directions. The smaller vessels form incomplete vortices, since they do not receive branches from all

directions. The larger ones, on the other hand, receive branches on all sides from the true choroid, the ciliary body, and the iris. Their ramifications form very numerous anastomoses, and cross the straighter ciliary arteries generally at very acute angles. Each vortex forms with its neighbor in the posterior regions of the choroid looped anastomoses, which often receive also a number of straighter branches from the anterior portions of the eye. The veins of the iris, the ciliary processes, and a portion of the veins of the ciliary muscle run backwards as numerous parallel and freely anastomosing vessels of about equal size, through the orbiculus ciliaris (smooth portion of the ciliary body) to the choroid. Within the limits of the ciliary body they all lie on the inner surface of the membrane, and only after crossing the ora serrata pass to the external surface of the choroid. They unite gradually to form still larger vessels, and, arrived within the choroid, combine in trunks which represent the proximate branches of the venæ vorticosæ.

These parallel veins of the orbiculus ciliaris, between which run at wide intervals the arteriæ recurrent., were formerly for the most part taken for arteries, and gave occasion to the acceptance of the so-called anterior branches of the art. cil. post. brev.

Only a portion of the veins of the ciliary muscle are united in the small ven. cil. ant., *c'*, which perforate the sclerotic in the vicinity of the corneal margin, and empty into the veins of the recti muscles.

These veins are in communication with the vascular circle of veins, *u*, which lies in the deepest layer of the sclerotic, just at the corneal margin. This circle was discovered by Schlemm, and is generally known by the name canalis Schlemmii; it is also called circulus, or sinus venosus corneæ, and by me *plexus ciliaris venosus.** This is not in fact a simple canal, but a plexus-like circle of veins (Rouget†), which, however, in different eyes, and in different regions of the same eye, presents a somewhat different aspect. As a rule, we doubtless find a large, flattened, and thin-walled vein, perhaps $\frac{1}{4}$ mm. in breadth, corresponding to the usual description; but this is accompanied on almost all sides by one or even several small veins, which branch off from it, and after a short course unite with it again. In many places the larger vein may divide into two, three, or more corresponding smaller veins, which anastomose with one another and gradually unite again to form a larger vessel. Very often the two branches formed by this division unite again immediately, so that in the course of the broad vein a little island, so to speak, is enclosed. More seldom we find a larger number (5–7) of smaller separate veins, freely anastomosing with one another, and running alongside of or partially overlapping one another, so as to form a beautiful plexus, which, however, gradually resolves itself again into a single larger vessel.

The plexiform character of the vascular circle is not equally developed in all eyes; it presents itself especially at those points of the circumference where the veins proceeding from the ciliary muscle unite with it. These at the anterior end of the muscle pass to the inner surface of the sclerotic (in one case I counted 12–14 of them), and separate in the vicinity of the venous circle into several anastomosing branches, a part of which perforate the sclerotic diagonally to join the episcleral venous plexus (see below) and the veins of the recti muscles, and a part empty into the circulus venosus. The latter often appears to be widened at these points, being directly continuous

* Loc. cit., p. 19, *Abbildung*, Taf. iii., und *A. f. O.*, xi. 1, Taf. ii. fig. 2.
† Rouget, *Compt. rend.*, et *Mém. de la Soc. de Biologie*, 1856, p. 118.

with the venous network of the ciliary muscle, or it presents a circular plexus of veins.

In perpendicular sections through the region of the corneal margin, especially in injected preparations, we almost always find near the one large vessel one or more smaller ones, or we may find two or more vessels which not infrequently anastomose with one another.

The venous circle of Schlemm appears to present a kind of reservoir for the blood of the ciliary muscle when it is in a state of contraction. In view of its situation, the contraction of the muscle might easily cause an expansion of its vessels.

In most animals a circular venous plexus is found in the corresponding place (Rouget, G. Meyer, Iwanoff, and Rollett).

In the above I think I have avoided the reproach which Henle* cast upon my former description, namely, that I placed too much stress upon the plexiform character of the circulus venosus. I was never of the opinion, as Henle† seems to think, that the circle was everywhere made up of a large number of smaller vessels.

The confounding of the circulus venos. with the so-called canal of Fontana (which occurs in the Ox, but not in Man) gave occasion to great perplexity in former times, and more recently led Pelechin‡ also into error; this mistake was long ago corrected by Brücke§ and Rouget,‖ and lately by Iwanoff and Rollett.¶

An analogue of the peculiar areolar tissue which occupies the space of Fontana exists, according to these authors, also in Man, although to a much less extent; this is the so-called ligamentum pectinatum, which extends from the edge of the membrane of Descemet across the circulus venosus to the insertion of the ciliary muscle and the origin of the iris.

The circ. venos. in Man may be injected from the vessels of the arteria as well as the vena ophthalmica,** although not easily without extravasations. The plexiform character of the venous circle may be more or less hidden by such extravasations, but these may be easily recognized by the absence of sharp borders. Extravasations take place even more easily by the old method of injection by puncture, in which quicksilver was generally used. Nevertheless, I have recently found that injections of glycerine colored with Berlin blue made in this way fill the venous circle with the greatest ease, and, in part at least, without extravasations; the injection-mass also passes into the finest ramifications of the episcleral veins and those of the ciliary muscle, even with moderate pressure.

These experiences with injections, the occasional containing of blood in the cadaver, especially in those who have died by hanging (Schlemm), and the existence of a thin vessel-wall, which may be easily demonstrated in cross-sections, ought, when taken together, to be considered conclusive proof

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* *Jahresber. über d. Fortschr. d. Anat. pr.* 1865. *Zeitschr. f. rat. Med.* 3, xxvii. p. 96–97.

† *Handbuch d. Anat.*, iii. 1 (Gefässlehre), p. 344 in der Note.

‡ "Ueber den sog. Kanal von Fontana od. Schlemm," im *A. f. O.*, xiii. 2, p. 425.

§ *Anat. Beschr. d. menschl. Augapf.*, p. 52 and 53.

‖ Loc. cit., p. 117.

¶ Iwanoff and Rollett, "Bemerk. zur Anat. d. Irisanheftung," etc., *Arch. f Ophth.*, xv. 1, p. 23.

** If this did not succeed with Pelechin (loc. cit., p. 440), I can only mention in opposition my own experience, according to which the filling of the circ. venos. is the rule in injections otherwise successful.

of the vascular nature of the circulus venosus; though this is still doubted* by many.

C. The Corneal Margin.

On the anterior portion of the sclerotic, where it is covered with conjunctiva, as far forward as the corneal margin, two vascular layers may be distinguished: a deep *episcleral or subconjunctival* layer, formed by the ramifications of the anterior ciliary vessels, and a superficial or *conjunctival* layer of vessels, which communicates with the former only at the margin of the cornea.

The *anterior ciliary arteries*, after their departure from the muscle, usually take a very tortuous course toward the corneal margin, giving off a number of fine episcleral branches, while their principal branches perforate the sclerotic. As a rule, two vessels arise from each muscle, but from the rectus ext. generally only one. In many cases an artery arises from the palpebral vessels on the lateral side and takes its course in the conjunctiva, to pass through the sclerotic only at a short distance from the corneal margin.

The *anterior ciliary veins* are distinguished from the arteries by their inferior size (since the perforating branches are much smaller), and by the straighter course of their more important branches. Their episcleral branches, on the contrary, surpass those of the arteries in thickness, according to the rule in cases where the region of ramification is the same. They are bound together by a highly developed network of fine veins with rather close polygonal meshes, which, from its location, has received the name of episcleral venous plexus, and which surrounds the corneal margin for a distance of about 4 mm.

The *episcleral branches of the arteries and veins* correspond pretty well in their ramifications; the arteries are always finer and take a straighter course than the veins, thus contrasting with the relations of the main trunks.

After the distribution of small twigs to the sclerotic they pass with continuous division and numerous curved communications toward the margin of the cornea, and here give off, at regular intervals, fine branches to the conjunctiva, namely:

The *anterior conjunctival arteries and veins.* These curve around, and pass backwards to supply the most internal zone of the conjunctiva, 3–4 mm. in breadth, and anastomose with the peripheral or *posterior conjunctival vessels.* The veins constantly accompany the arteries here, one upon either side.

The ends of the episcleral vessels, constantly dividing and anastomosing, run across the corneal margin, and form the *marginal looped plexus of the cornea*, which occupies the most peripheral zone of the cornea for a breadth of 1–2 mm., being generally somewhat broader above and below than at the sides. In the capillary loops may be distinguished a smaller ascending, arterial, and a descending, gradually increasing, venous trunk.

The Human cornea contains after birth no vessels which penetrate farther towards its centre.

In the fœtus, H. Müller found vessels over the entire anterior surface of the cornea. In many animals, for instance, in Sheep and Oxen, the vessels, even in the adult state,

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* Just after writing these lines the work of Schwalbe appeared, "Ueber die Lymphbahnen des Auges und ihre Begrenzung," in the second part of which (M. Schultze's *Archiv*, vi. p. 261–362), the author declares the canal of Schlemm to be a lymph-space, and separates it entirely from the ciliary plexus. In opposition to him I must support the opinion above expressed.

reach much farther into the cornea. In the Ox one may clearly distinguish superficial marginal loops with flat arches from deeper vascular loops, which advance much farther into the cornea in company with the nerves. In the Sheep, Coccius saw these vessels passing as far as the middle of the cornea.

Newly-formed vessels very often make their appearance in keratitis; they may be located in all the layers of the cornea.

III. Vascular System of the Conjunctiva.

The larger peripheral portion of the scleral conjunctiva, the palpebral folds, and the tarsal portions of the conjunctiva are supplied by the vessels of the lids, the arteriæ palp. med. and lat., and their corresponding veins.

A number of small arborescent vessels, art. and ven. conj. post. fig. 1, *d*, *d*, pass to the scleral conjunctiva at the palpebral folds. The arteries, like the anterior conjunctival vessels, are accompanied in their ramifications by one or two veins. Their ends anastomose with those of the anterior conjunctival vessels. The capillary network is rather loose, but becomes finer towards the palpebral folds, and reaches its highest development in the small papillary elevations of the tarsal conjunctiva.

The posterior conjunctival vessels, and more especially the veins, are visible in the living Human eye as small vessels movable with the conjunctiva, and are to be distinguished from the anterior ciliary arteries not only by their course but also by their bright-red color and their inferior calibre; the latter have more of a carmine-red color, and are not movable with the conjunctiva. The difference in color is caused by the fact that the latter vessels are covered by the whitish, cloudy conjunctiva. The anterior conjunctival vessels are scarcely visible, owing to their fineness; so also the anterior ciliary veins, but these are plainly to be seen when the eye is irritated, being then considerably enlarged. The injection of the episcleral venous network occasions at the circumference of the cornea a diffuse, bluish-red color, which, in pathological conditions, indicates an irritation of the parts supplied by the ciliary vascular system, namely, of the uveal tract or the cornea.

IV. THE LYMPHATICS OF THE EYE.

By G. SCHWALBE.

The lymph formed in the tissues of the eye passes out of the eyeball in three different directions. That portion of it which has its origin in the iris and ciliary processes is at first collected in the anterior chamber of the eye, which has its outlet in the vicinity of the canal of Schlemm. The canal of Petit is in direct communication with this system. We may designate these passages, including the lymphatics of the conjunctiva, and the canaliculi of the cornea, as the anterior lymphatics of the eye. All the portions of the eye posterior to the ciliary body discharge their lymph by two other ways; the choroid and sclerotic by outlets not far from the points of exit of the venæ vorticosæ, and the retina, on the other hand, by an independent passage within the optic nerve. These two latter systems may be considered as the posterior lymphatics of the eye, and to them may be added still another lymph-space, which is situated between the two sheaths of the optic nerve.

1. The Posterior Lymphatics of the Eye.

a, *The Outlet for the Lymph Formed in the Choroid and Sclerotic.*

Lymphatic vessels are as little to be found in the true tissue of the sclerotic as in the vascular layer of the choroid. The lymph formed in these membranes passes first into two large fissure-like spaces, which are in direct communication with one another (compare fig. 335). One of these spaces (p) is to be found between the sclerotic and choroid throughout the whole extent of these membranes, from the ciliary body quite to the vicinity of the entrance of the optic nerve into the bulbus. This has been called the *perichoroidal space*, because it surrounds the choroid. In Birds it exists in the form of a fissure, with two smooth walls, after the manner of the serous cavities. In Mammalia there are generally to be found between the two membranes numerous bands of connection, which in many eyes (the Dog, Man) may be developed into a rich network, known as the *membrana suprachoroidea.* That part of this tissue which remains adherent to the sclerotic when the choroid is torn off is called also lamina fusca.

Fig. 335.

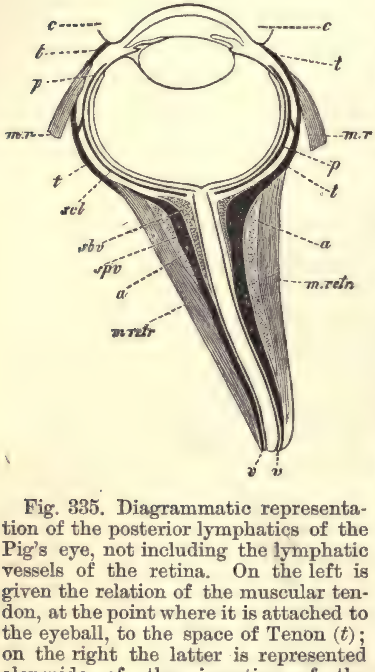

Fig. 335. Diagrammatic representation of the posterior lymphatics of the Pig's eye, not including the lymphatic vessels of the retina. On the left is given the relation of the muscular tendon, at the point where it is attached to the eyeball, to the space of Tenon (t); on the right the latter is represented alongside of the insertion of the muscle. The explanation of most of the letters is to be found in the text. In addition, a indicates a layer of fat between the musculus retractor and the supravaginal space; c, the conjunctiva; m, r, musculi recti; m, retr. musculus retractor bulbi; v, external or fibrous sheath of the optic nerve.

The structure of the meshwork of the suprachoroidea is as follows:—it consists of numerous, very flat lamellæ, the groundwork of which is formed by a rich network of elastic fibres. Closely attached to this network are numerous, very flat, more or less branched pigment-cells, which often, when many lie too close together, assume an arrangement similar to that of epithelial cells. In many animals, in the Pig, for example, some small, flat, colorless cells are always to be found with the pigment-cells. Both sides of the thus formed elastic lamella, or, where this lies close against the sclerotic, only one side, are covered by a very thin, transparent membrane, which is interspersed from place to place with ellipsoidal nuclei projecting above the level of the membrane. If these membranes are treated with $\frac{1}{4}$–1 per cent. solutions of nitrate of silver, they display upon their surface a beautiful network of black, silvered lines, in which each mesh corresponds to one of the ellipsoidal nuclei. The elastic lamellæ of the suprachoroidea are therefore covered with an endothelium which differs but little from that of the other lymph-passages. This may be demonstrated as well on the external

surface of the choroid as on the internal surface of the sclerotic, extending continuously throughout the entire perichoroidal cavity.

When injections of the perichoroidal space are made, it is to be remarked that the injected substance passes out into the second of the above-mentioned fissure-like lymph-spaces at four points on the surface of the eyeball, and these points lie just behind the points of exit of the venæ vorticosæ. A more careful examination of this region shows that the lymphatic vessel at first surrounds like a sheath the vein as it passes obliquely through the sclerotic (fig. 336); but shortly before its appearance upon the surface of the eyeball it betakes itself quite to the under and inner side of this blood-vessel. Its course through the sclerotica is therefore in a great degree perivascular. Arrived on the surface of the bulbus, the injecting substance spreads out in a lymph-space, which is situated between the sclerotic and the fascia of Tenon, and which may be designated as the *space of Tenon* (fig. 335, *t*). This is lined throughout with an endothelial layer of cells similar to those of the perichoroidal space. By the use of nitrate of silver a network of black, silvered lines may be demonstrated on the surface of the sclerotic. At those places where the muscles are attached to the eyeball, the space of Tenon suffers an interruption; it is not, however, continued into the sheath of the tendon, but is completely shut off in this direction. In the Mammalia it is divided into an anterior, larger, and a posterior, smaller, section by the musculus retractor bulbi (fig. 335, *m, retr.*)

Fig. 336.

Fig. 336. Diagrammatic drawing representing the passage through the sclerotic of a vena vorticosa, with its perivascular space, taken from eye of the Pig. *r*, retina; *ch*, choroid; *pch*, perichoroidal space, injected; *scl.* sclerotica; *t*, space of Tenon; *v*, vena vorticosa.

At the posterior pole of the eye, about the point of entrance of the optic nerve, the space of Tenon is in communication with another lymph-space, which surrounds, after the manner of a sheath, the external fibrous sheath of the opticus, and which, from its situation, may be called the *supravaginal space* (fig. 335, *spv.*) This space opens finally through the canalus opticus into the arachnoidal cavity of the brain, which latter is in direct communication with the lymphatics of the neck, as is demonstrated by injections under the dura mater.

b, *The Lymphatics of the Retina.*

The lymphatics of the retina surround the blood-vessels of this membrane in the form of sheaths, as was discovered by His (7 and 8): they are perivascular canals of the same nature as those which were demonstrated by the same investigator in the brain and spinal cord. The veins and capillaries are surrounded completely by these lymphatic sheaths, while the arteries are probably accompanied by the lymphatic vessels only in the form of striæ. An injection of the lymph-passages of the retina may be accomplished by pressing the injecting fluid into the blood-vessels with great force. The latter are thus torn at some points, and the fluid spreads from these rents throughout the perivascular canals. The outflow of the retinal lymph takes place through the lamina cribrosa into the

opticus. Concerning the further course of this outlet nothing more definite is known. According to His, the external portion of the optic nerve contains a rich plexus of lymphatics, which, however, no longer assume the perivascular arrangement.

Probably, also, a space described by Henle and Merkel (9), which lies between the limitans interna and the layer of optic-nerve fibres, is in connection with the perivascular canals of the retina. In this space lymph corpuscles have been found, but injections of it have not proved successful.

It is still unknown what relation the tissue of the vitreous body holds to the lymphatic system. Stilling (11) found that there exists in the Pig's eye a central canal running from behind forwards, which may be easily filled with carmine solution dropped upon the posterior surface of the vitreous; this space he holds to be a lymph canal. The perivascular canals of the Frog's hyaloidea, described by Iwanoff (10), are the analogues of the perivascular canals of the mammalian retina.

c, A lymph space, which has no connection with either of the systems just described, is to be found between the two sheaths of the opticus throughout its whole extent from the bulbus to the canalus opticus. This, from its situation under the fibrous sheath of the nerve, may be described as the *subvaginal space* (fig. 335, *sbv*). At the entrance of the optic nerve it extends to a point just beneath the choroid, without, however, entering into communication with the perichoroidal space. Its walls are covered by an endothelium, which may easily be resolved into small nucleated plates; the walls are also united by an abundant network of delicate connective-tissue trabeculæ, which are likewise surrounded by sheaths of endothelium. Such sheaths may often be completely isolated, and then present themselves as perfectly transparent membranes interspersed with oval nuclei.

2. The Anterior Lymphatics of the Eye.

a, The Lymphatic System of the Anterior Chamber.

The anterior chamber of the eye is a reservoir for the lymph arising from the iris and ciliary body. The influx into the anterior chamber takes place at two points: from the canal of Petit through the capillary fissure between the pupillary margin of the iris and the anterior capsule of the lens, and, secondly, through the interstices between the trabeculæ of the ligamentum pectinatum.

The canal of Petit runs around the margin of the lens, and extends laterally in the form of a fine fissure as far as the ora serrata. It communicates with the posterior and through it with the anterior chamber by a series of minute orifices, which are to be found in the zonula ciliaris close to the edge of the lens. It may be very easily injected from the anterior chamber, especially in the eye of the Pig. Under normal conditions, however, a passage of fluid can only take place from the canal of Petit towards the anterior chamber, but not in the opposite direction, since in the latter case the iris forms a valve-like obstruction, which can only be overcome by a change in the shape of the eyeball dependent upon increase of intraocular pressure, such as is caused by injection of the anterior chamber.

The great mass of the lymph coming from the ciliary body, and probably also from the iris, enters the anterior chamber by the interstices between the trabeculæ of the ligamentum pectinatum. We have as yet only in the Pig's eye succeeded in filling a portion of this region with soluble Berlin

blue injected into the anterior chamber; the injection fills a fissure, which is traversed by a network of connective tissue, and which surrounds the space of Fontana, extending backwards to the posterior end of the ciliary body where it lies between the ciliary muscle and the pars ciliaris retinæ. In the human eye also the injecting fluid may be forced for a certain distance into the ciliary body at this point. The trabeculæ of the space of Fontana in the Mammalia, as well as the corresponding trabeculæ of the ligamentum pectinatum in Man, are invested by a complete endothelial sheath, which is precisely similar to that covering the trabeculæ of the subvaginal space.

In order to become acquainted with the manner in which the communication takes place between the human anterior chamber and the veins, it is necessary to examine meridional sections through the corpus ciliare of eyes, in which the veins have been filled by injections forced into the anterior chamber. In such sections it is to be remarked in the first place, that a short stripe of the blue mass passes just behind the border of Descemet's membrane from the anterior chamber obliquely backwards and outwards to the canal of Schlemm. The latter is also completely filled with the injection. In many preparations we may observe injected vessels, arising from the canal of Schlemm and passing backwards and outwards through the sclerotic. These vessels are veins, as is proved by an exact histological examination. The canal of Schlemm, on the contrary, must undoubtedly be considered as a lymph-space, since in the character of its walls it differs essentially from the veins. It communicates with the anterior chamber by a system of fine fissures. These fissures are to be found between the elastic circular fibres and fenestrated membranes, which stretch from the border of Descemet's membrane, as its modified prolongation, to the most posterior point of the insertion of the ciliary muscle, and interiorly are in connection with the meshwork of the space of Fontana. This peculiar tissue bridges over a groove, which runs along the inner surface of the anterior extremity of the sclerotic just at the line of its junction with the cornea, thus constructing a fissure-like circular canal. The latter is no more or less than the canal of Schlemm. The ciliary plexus of Leber lies, as this author himself states,* in the compact tissue of the sclerotic just exterior to this groove.

In many cases you may find instead of one open lumen two or even more of them, thus forming a transition to the eyes of the Mammalia, in which are always to be found, at the corresponding place, several smaller lumina, which, however, are always situated internal to the scleral groove.

It is still unknown in what manner the canal of Schlemm is in communication with the neighboring veins. Probably there here exists a valvular arrangement, which in normal conditions of tension hinder the passage of venous blood into the canal of Schlemm.

If we reflect what would be the consequences if the anterior chamber possessed ready outlets in the form of lymphatic vessels, we shall easily comprehend the purpose of the above-described arrangement. If the humor aqueus were carried off by lymphatic vessels, it is obvious that a proper degree of tension could not be maintained in the anterior chamber; since, owing to the low degree of pressure in the lymphatic vessels, a rapid outflow of the humor aqueus must take place, which could not possibly be compensated for by the transudation of fresh fluid from the vessels,

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* "Anatomische Untersuchungen über die Blutgefässe des menschlichen Auges," *Denkschr. der Kais. d. Wissensch. zu Wien.* Math.-naturw. Classe. Bd. 24, p. 316.

and as a consequence the anterior chamber would collapse. This is, however, guarded against by the discharging of the anterior chamber into the veins through the medium of the canal of Schlemm. Thus it is rendered possible for the tension of the anterior chamber to be maintained at its height, the flow to and from it being kept at an equilibrium, by the fact that the pressure in the small veins is considerably less than in the corresponding lymphatic vessels, and also by the obstacles, namely, the system of fine fissures, which are encountered by the fluid in its passage from the anterior chamber to the canal of Schlemm.

b, For the *canalicular system of the cornea*, see the description of the cornea in this text-book.

c, *The Lymphatics of the Conjunctiva.*

The lymphatics of the conjunctiva were discovered by F. Arnold (5), and more accurately described by Teichmann (6). They arise from the margin of the cornea, where they form a fine plexus, about 1 mm. in breadth, communicating externally with the more widely meshed lymphatic plexus of the conjunctiva scleroticæ. In this the trunks soon increase in size and take a course for the most part meridional, anastomosing with each other by numerous short and thinner transverse branches. According to Teichmann, a few branches, about 0.1 mm. in diameter, run from the fine plexus at the corneal margin in a meridional direction towards the centre of the cornea. These perhaps correspond to the appearances at the margin of the cornea resembling vessels, and supposed to be lymphatic vessels, described by Kölliker (3), His (1), and Sämisch (2).

According to Lightbody (4), the capillaries of the corneal margin are surrounded by lymphatic sheaths. I have been unable, however, to convince myself of the correctness of this statement.

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V. THE VITREOUS BODY.

By Prof. A. IWANOFF.

The vitreous body occupies the greater part of the cavity of the eyeball, and is bounded posteriorly and laterally by the retina. Its anterior surface is hollowed out to form a dish-shaped excavation (fossa patellaris), in which lies the lens enclosed in its capsule. From the border of the lens to the summits of the ciliary processes its surface is free, and turned towards the zonule of Zinn. The interspace bounded by this free portion of the surface of the vitreous and the zonula Zinnii is called the canal of Petit, which surrounds the entire free equatorial border of the lens.

The dimensions and relations of this canal (canal godronné, Petit) in the living subject are not as yet sufficiently understood. Even Brücke assigned to this canal a much smaller space than was given it in the original description of Petit. Henke goes still further; he denies entirely the existence of such an open space in the living eye: "It is plainly to be considered," says he,* "not as a true cavity, but only as a fissure between two free (serous) surfaces, which are movable one upon the other, but which enclose no interspace, like the cavities of the pleura, the peritonæum, and the joints." Henle is of the same opinion, while Kölliker, on the other hand, believes that the canal is certainly very narrow, but in the living eye possesses an open lumen and contains moisture.

My own investigations confirm the views of Henle; at least I found it impossible in frozen eyes to find ice in the canal.

The corpus vitreum is not, as has hitherto been generally believed, surrounded by a special membrane, the so-called membrana hyaloidea. The membrane formerly called hyaloidea is identical with the membrana limitans retinæ. It is a constituent part of the retina, and therefore is in direct apposition with the vitreous only so far as the retina extends, namely as far as the ora serrata. The limitans, it is true, is continued upon the pars ciliaris retinæ, but in this region there lie between the vitreous and the limitans certain meridional fibres, which have received the name zonula Zinnii, and which are attached to the limitans as well as to the vitreous.

In the vicinity of the ciliary processes the vitreous separates itself from the zonula, so that its entire anterior surface, or that which is turned toward the canal of Petit and the lens, is not covered by any special membrane;

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* Graefe's *Archiv*, vi. 2, p. 61.

neither by a prolongation of the limitans, as stated by Henle, nor by a special membr. hyaloidea, as was formerly supposed.

The non-existence of the hyaloidea was pointed out by Henle.* Nevertheless the designation limitans hyaloidea is not quite proper in a strictly anatomical point of view. That the limitans is an integral part of the retina is most clearly demonstrated by the pathological processes which take place in the corpus vitreum, as a consequence of which the latter shrinks up and detaches itself from the retina.† In such cases the limitans is always found adherent to the retina.

In the quite fresh, and even better in the hardened, corpus vitreum, the peripheral portions present distinct differences from the central portions. In the former may be remarked a more or less marked lamellar structure, while the latter seems homogeneous.

Stilling designates the central portion as nucleus, and the peripheral portion as cortex. The homogeneous central portion, the nucleus, does not lie in the middle of the organ so as to be uniformly surrounded by the concentric lamellar cortex, but is pushed forwards toward the lens in such a manner that the cortical substance becomes anteriorly more and more thin. Thus at the ora serrata the several concentric layers of the cortex are so crowded together, that the surface of the nucleus is separated from the limitans only by a very thin, but plainly fibrous layer. The fibres of this layer run parallel to the surface of the vitreous in wavy bundles, and are not unlike bundles of connective tissue. The entire layer, thus changed, finally turns and passes towards the axis of the eye, thus completely covering the anterior surface of the vitreous.

Since we here in fact have not a single but several layers crowded together, and only loosely united with one another, it is easy to see how one might suppose that behind the lens there lay a special membrane covering the corpus vitreum, especially since the most superficial of these layers is perfectly smooth. The deeper layers may sometimes be separated from one another in hardened eyes, which circumstance led Hannover and Finkbeiner ‡ to the opinion that the hyaloidea again divided itself into two layers on the anterior surface of the vitreous, in such a manner as to form behind the canal of Petit a second canal (the canal of Hannover).

In the anterior portion of the vitreous we find in the cortical layer, besides the already mentioned fibres resembling connective tissue, also a considerable number of other fibres not unlike the elastic fibres. They begin as exceedingly fine tortuous fibres, as far back as the equator of the eye; at the ora serrata they appear in greater numbers, and from this point onward they curve in upon the pars ciliaris retinæ, lying close against the limitans, and here form the beginnings of the zonula Zinnii.

A canal of about 2 mm. in diameter runs directly through the vitreous body from the papilla optica to the posterior surface of the capsule of the lens.

The difficulties which stand in the way of the examination of the corpus vitreum in the fresh state gave occasion to the fact that all the earlier anatomists, who made it a special object of study, employed artificial methods of hardening. It was supposed, indeed, that the different working of chemical reagents upon the stroma and the mucous fluid contained within its meshes would be able to separate them one from the other.

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* *Eingeweidelehre*, p. 661.

† "Beiträge zur norm. u. path. Anat. d. Auges," von Iwanoff; *A. f. O.*, xv. 2, p. 51.

‡ Comp. "Untersuchungen der Stärke des Glaskörpers bei den Wirbelthieren." *Ztschr. f. w. Zoologie*, vi. p. 335.

Pappenheim * was the first to adopt this method. He found, by hardening the vitreous in carbonate of potash, that the stroma of the organ consisted of layers running parallel to the surface of the hyaloidea, and composed of very fine fibres, and a homogeneous substance; Brücke † found, by treatment with acetate of lead, that the vitreous is composed of a great number of very thin structureless membranes, which are enveloped one within the other like the layers of an onion, and which take a course parallel to the surface.

According to Hannover,‡ such a structure is only to be found in the Mammalia; in Man the vitreous, according to his statements, consists of sections which are arranged in a radial manner about the optic axis, so as to present a resemblance to the structure of the orange. All this, however, is observed only in eyes which have been for a long time exposed to the action of diluted chromic acid.

Finkbeiner confirmed all the views of Hannover by examinations of the vitreous which had been treated with corrosive sublimate.

Bowman,§ Doncan, Virchow, Kölliker, and Henle, on the other hand, arrived at entirely negative results. Bowman and Doncan, when they attempted to confirm the researches of Hannover and Brücke, found no membranes at all in the vitreous; in their opinion the membranes, and their arrangement as described by those authors, are to be considered as artificial appearances produced by the working of different reagents; Doncan inclined to the views of Virchow and Kölliker, the first of whom reckoned the vitreous as mucous tissue, the latter as connective substance. Nevertheless, he does not deny the fact that neither the existence of fluid and solid elements in the vitreous nor the entoptic phenomena are thus sufficiently explained. Henle also found no membranes, and describes the corpus vitreum simply as a homogeneous substance of gelatinous or cellular nature.

Weber arrived at quite peculiar conclusions, and different from the views of all other authors. According to him the entire vitreous consists of a network of cells, which anastomose with one another, and in whose meshes a mucous fluid is contained.

Smith, ‖ who macerated the human vitreous in water for several days, and then treated it with carbolic acid, recently stated that the peripheral portion of the vitreous possesses a concentric, and the central portion a radial structure; according to him the concentric layers consist of coarser fibres, and the nucleus, of stellate anastomosing cells. He noticed also an open canal stretching from the papilla optica to the posterior surface of the lens.

Bowman previously made similar statements with regard to the central portion. With the method adopted by Smith, it is difficult to decide what appearances may and what may not be due to artificial means.

The great diversity of opinions held by the various authors, as exhibited in this brief historical notice, is to be explained partly by the difficulty which is encountered in the examination of the fresh vitreous, and partly by the general distrust of the various methods of artificial hardening.

The principal object of all the controversies are the membranes. Some affirm that all the layers of the vitreous are separated by membranes; others, because they find no membranes, deny the accuracy of all the other observations. The membranes do not exist, but the possibility of a lamellated structure is therefore by no means to be excluded. In thin transverse sections of eyes hardened in Müller's fluid the vitreous is resolved into layers which run parallel to its surface; with the aid of high powers, and after coloring with carmine, a finely granular mass is to be seen in the posterior portion of this organ, in which fine fibres are occasionally to be recognized. In the anterior part these fibres gradually increase in size as they approach the ora serrata, and finally take a wavy course parallel to the surface. Here also there is no trace of a membrane to be seen.

All these views concerning the structure of the corpus vitreum receive fresh confirmation from the researches of Stilling,¶ the excellence of which lies in the fact that they were made only on the vitreous in the fresh state, and therefore are not open to the objection that their results may have been artificially produced. According-

* *Spezielle Gewebelehre d. Auges.* Breslau, 1842, p. 182.

† Müller's *Archiv*, 1843, p. 345.

‡ Müller's *Archiv*, 1845, p. 467. *Das Auge. Beiträge zur Anat., Physiol. und Pathol. dieses Organs.* Leipzig, 1852, p. 18.

§ Froriep's *Notizen*, No. 238. Dec., 1849, p. 274.

‖ D. Smith, "Structure of the Adult Vitreous Humour." *Lancet*, Sept. 19, 1868, p. 376–378.

¶ "Eine Studie über den Bau des Glaskörpers." *A. F. A.* xv. 4. Heft.

ing to his statements, if we make a section through the fresh organ perpendicular to the optic axis, and let a few drops of carmine solution fall upon its surface, a number of concentric furrows, 6–12 in number, will make their appearance in the periphery; the middle, or the nucleus, on the contrary, will remain free from any such appearance. The furrow which forms the boundary-line between the cortex and nucleus is generally the deepest, and soonest filled with the coloring fluid. Stilling does not describe the relations of the cortex and nucleus quite correctly, since his method of examination could only reveal the coarser appearances; according to his statements the cortex is applied to the nucleus only commencing at the ora serrata, so that the lens and zonula are in apposition with the nucleus itself. As we have seen above, the cortical substance surrounds the nucleus throughout its whole extent, certain of its layers being tightly crowded together anterior to the ora serrata, exactly as is represented by the drawings of Hannover and Finkbeiner.

After Henle had called attention to the fact that the membrana hyaloidea did not exist, he sought to explain the existence of the membrane which, in his opinion, covered the vitreous in the fossa patellaris. According to him the limitans, even before it reaches the ora serrata, increases in thickness, and at the same time changes the character of its tissue; here and there it is resolved into fibres, which sometimes take an irregular course, like the fibres of elastic tissue, sometimes a parallel and wavy course, like the fibres of connective tissue. These fibres are always exceedingly fine, and while the larger number of them pass along the surface of the vitreous, some penetrate into its interior, where they are soon lost.

The superficial fibrous tissue of the limitans hyaloidea is divided, according to him, into two membranes, at the point where the orbicularis ciliaris begins to swell out into the corpus ciliare: one membrane passes inwards, to form the hyaloidea of the fossa patellaris, and the other passes outwards to the pars ciliaris retinæ, to form the zonula.

From the preceding researches it is to be remarked, in opposition to the views of Henle, that all those changes which Henle attributes to the limitans, take place in the peripheral layers of the vitreous, while the limitans itself remains unchanged, and, becoming gradually thinner, simply passes from the ora serrata over upon the pars ciliaris retinæ. It takes, therefore, not only no part in the formation of the hyaloidea of the fossa patellaris, which as was shown above does not exist, but even its participation in the formation of the zonula is more than doubtful. I at least have never been able to recognize such a relation, while the origin of the zonula in the vitreous is very easy to observe.

There remains, therefore, to be decided only the question whether the limitans is in reality continued over the pars ciliaris retinæ. Henle himself says, that if the fibrous layer of the zonula is to be considered as anterior fold of the limitans, the latter must at the summits of the ciliary processes again divide into two folds, and he has even seen in some cases that the vitreous membrane stretched over the origin of the fibres of the zonula upon the orbiculus ciliaris.

This vitreous membrane is obviously the limitans itself, which is continued beyond the ora serrata upon the pars ciliaris; Kölliker is also of this opinion. In meridional sections through the pars ciliaris this limitans is very easily seen, that is, if the section runs exactly parallel to the fibres of the zonula. In such preparations the limitans appears as a distinct line of double contour, which separates the pars ciliaris retinæ quite sharply from the zonula. In carefully made preparations the limitans may be separated as a fine membrane for a certain distance from the zonula as well as from the pars ciliaris retinæ.

In regard to the development of the zonula, we only know that it does not exist in the embryo so long as the vessels surrounding the capsule remain, although even at this period the limitans is completely developed. The zonula begins to be formed at the time when the vessels of the capsule are receding, and becomes plainer as they become more atrophic.

If, however, the unchanged limitans is prolonged from the ora serrata upon the pars ciliaris retinæ, it is plain that it cannot also form a mass of zonula fibres, and, in addition to this, the membrane of the fossa patellaris, by a repeated subdivision.

All this confusion was occasioned by the fact that it was not remarked that, even before arriving at the ora serrata, the superficial layers of the vitreous change their structure, and are closely united with the limitans and the retina. This union, however, is not indissoluble, and in certain pathological conditions, and also in healthy eyes, by the use of alkalies, we may succeed in separating the vitreous with the zonula from the limitans.

Martegiani, in 1814, described in the vitreous, at the point of entrance of the optic nerve, a funnel-shaped excavation, which he designated as "area." This area of

Martegiani is in fact the commencement of the canal, which has improperly been called canalis hyaloideus Cloqueti. Cloquet never saw or described this canal in the adult; he describes only the course of the arteria capsularis in the fœtal vitreous.

Hannover described it better, but expressly says that he never found it pervious, and therefore he knew nothing of the existence of a true canal.

The descriptions of Finkbeiner * are not clear; he says, in fact, nothing of an open canal existing in every adult Mammalian or Human eye. He describes satisfactorily only an eye of the Ox, in which two lengthened areæ unite to form a solid string which traverses the corpus vitreum.

Stilling first called attention to this canal as being pervious, and existing in every Mammalian and Human eye during its entire life, and as gradually increasing up to the time of perfect development of the entire eye. He also gave the methods by which the canal may be demonstrated in the fresh eye.

The cells of the corpus vitreum lie only in its external, superficial layers; in the deeper layers their derivatives only are to be met with, namely, nuclei and shrunken vesicles. Their form is very manifold; still they may all be included in three principal groups:—

1. Round cells with large nuclei; the latter being surrounded by coarsely granular protoplasm. These are met with mostly in the anterior portions of the vitreous, especially in Children, in whom they often contain several nuclei.

2. Spindle-shaped and stellate cells. These are found throughout the entire surface of the vitreous. The stellate cells generally possess long, fine, and branched processes, provided with varicose swellings.

3. A peculiar characteristic form of round cells, which contain in their interior a large, perfectly transparent, round vesicle. In the completely developed cell of this variety there is only a single vesicle, which fills up almost its entire space, leaving at the periphery only a little space for a nucleus, surrounded by a small quantity of protoplasm. Sometimes instead of one, two vesicles are to be found, separated by a straight line. In other cases several vesicles are to be found, which seem to be surrounded by a common envelope, with a regularly circular contour. These vesicles are to be found not only in the round cells; they occur also in the processes of the stellate cells. Here they sometimes reach colossal dimensions, so as to surpass in size the cell itself. This form is met with in every period of life, but most frequently in aged people, and generally in the posterior portion of the vitreous body.

All these cells possess the property of contractility; they change their form, and, perhaps, even their place. In the round cells, containing vesicles, the contractility is less in proportion as the vesicles are larger, that is, in proportion as the protoplasm has disappeared.

The views concerning the existence and nature of the cells are quite as diverse as those concerning the stroma.

The first special researches on the cells were made by Virchow. In the Pig's embryo, 4″ long, he found, at pretty regular intervals in the homogeneous intercellular substance, round, nucleated, and highly granular cells, sometimes containing several nuclei.

According to Kölliker, the cells are most generally found in young individuals; he saw them, indeed, in adults, but only in a few cases, and then scarce and indistinct, generally in the vicinity of the lens and the hyaloidea. Weber, on the other hand, found stellate, anastomosing cells throughout the entire vitreous. Hannover and Finkbeiner described an epithelium covering the hyaloidea, which, according to the latter author, also covers the several sheath-walls of the interior. Coccius is also of the same opinion. Ritter found an epithelium with branching cells only on the inner surface of the hyaloid, but not in the interior of the vitreous.

* L. c., p. 332.

The fibres of the zonula arise, as has been already intimated, from the vitreous body, and in fact from that portion of it which has not yet reached the ora serrata retinæ. In the vicinity of the latter the fibres of the zonula, which at first lie beneath the surface of the vitreous, pass up and apply themselves to the membrana limitans interna, with which they enter into intimate contact; thus at the ora serrata the vitreous and limitans find themselves so firmly united that, as is well known, the attempt to separate the retina from the vitreous does not succeed at the ora serrata, fragments of the vitreous always remaining attached at this point. But as on the one hand the existence of zonula-fibres may be with certainty demonstrated even posterior to the ora serrata, so also the district of its origin is not limited by the ora. On the contrary, the passage of zonula-fibres from the vitreous may be demonstrated for some distance anterior to the ora (or toward the ciliary processes), so that even in this region the zonula and vitreous are not isolated structures.

Not until it has reached a point 4–5 mm. distant from the ora serrata can the zonula Zinnii be considered as a completely separate structure. Throughout its course toward the lens it is separated from the pigment-layer of the smooth portion of the corpus ciliare, as well as from that of the processus ciliaris, by the pars ciliaris retinæ, and the everywhere demonstrable membrana limitans. The zonula, however, is not prolonged as far as the summits of the most anterior ciliary processes; it separates from them sooner to pass toward the equator of the lens. Arrived at this point, the fibres of the zonula divide up into brush-like processes, which attach themselves to the anterior and posterior capsule of the lens.

The first beginnings of the zonula-fibres in the vitreous make their appearance as wavy bundles of the finest fibrillæ. On the surface of the corpus vitreum, each bundle of fibrils coalesces to form a single fibre; the fibres thus formed are the finest fibres of the fully-developed zonula. In their passage out of the vitreous the fibrils (not yet blended) enter into a very intimate union with the limitans. Thus it happens that if we attempt to separate the zonula from the corpus ciliare backwards, it tears off from the limitans at the point in question. This is the foundation for the erroneous opinion that the zonula-fibres are immediate prolongations of the limitans. If, however, we macerate the vitreous with the zonula and lens for several weeks in a 10 per cent. solution of common salt, the union between the zonula-fibres and the limitans will be dissolved, so that these two structures may be easily isolated.

The fibres of the zonula as they advance toward the ciliary processes in part unite to form fibres gradually increasing in size, so that the free portion of the suspensory band of the lens (which aids in forming the posterior wall of the posterior chamber) contains the thickest fibres; in part, however, they run with almost unchanged diameter from the ora serrata to the equator of the lens. At this point they are again resolved into the finest fibrils, as mentioned above.

In meridional sections of the eye the zonula appears as if attached to the equator of the lens by a sort of triangular base. This triangular space is in reality filled with the terminal fibrils of the zonula-fibres, and therefore does not enclose a cavity; nor has it been taken for the canal of Petit by any one except Merkel.

The fibres of the zonula are neither fibres of connective tissue nor elastic fibres, being distinguished from them both by chemical (by their behavior, when treated with acids and alkalies) and physical peculiarities. To hold them for muscular fibres, as has recently been done, is downright audacity.

As yet researches in comparative anatomy and embryology, which alone should be relied upon to shed light upon the true nature of the zonula-fibres, are wanting.

The zonula Zinnii represents the anterior wall of the canal of Petit. Its posterior wall is formed by the smooth surface of the corpus vitreum. The tissue of the vitreous is here condensed to form a limiting layer, in the same manner as Bowman's membrane is formed by a condensation of the substantia propria of the cornea; an independent membrane—the hyaloidea—does not exist at this place. The canal of Petit begins 4–5 mm. from the ora serrata, and extends not only to the equator of the lens, but also for a distance of 2 mm. along the posterior capsule in the direction of the posterior pole of the lens.

It is difficult to accept the opinion that in the living eye there exists a space filled with fluid corresponding to the canal of Petit, that is to say, a lumen of this canal. It is much easier to believe, with Henke and Henle, that in the living eye the anterior and posterior walls of the canal of Petit are movable one upon the other, and, without being absolutely united, are separated only by an exceedingly thin layer of moisture. Although the canal of Petit, as such, may have no existence, still the physiological rôle devolving upon it, namely, that of assisting in the function of accommodation, might be fulfilled by the arrangement above described.

VI. THE LENS.

By Prof. BABUCHIN.

To the essential component parts of the dioptric apparatus of the eye belongs the lens, an organ which, by its form and transparency, reminds one very much of a glass biconvex lens, and which differs in shape in different animals. While in Man the axis of the lens is nearly a third smaller than the diameter of the equator, in many animals the lens acquires an almost globular form. But however various the form and dimensions of the lens may be, its elementary structure and the plan of its composition is always the same in all the vertebrate animals. It consists, namely, of two elementary parts: the cellular elements, which form, as it were, the body of the lens (parenchyma lentis, true substance of the lens), and an envelope, which exhibits no further histological element, and which surrounds the lens-body on all sides, and is called the capsule of the lens.

The body of the lens may be considered as consisting of two layers. One of these, the anterior layer, is very thin, and in the vicinity of the equator begins to increase in thickness, either very gradually, as in Man and the Mammalia, or quite abruptly, as in the Birds and the scaly Amphibia. The posterior layer, on the contrary, is very thick, being thickest at the axis of the lens and growing thinner as it passes toward the equator. In the region of the equator both layers blend with one another; in some animals farther forwards, in others farther backwards; or, more properly speaking, the layers pass over into one another by a rounded border. With the exception of

this border the two layers may be easily separated from one another throughout their whole extent, nevertheless there exists between them no appreciable interval (fig. 337).*

The anterior layer consists of flat, perfectly transparent, in the fresh state from the animal just killed, quite structureless, polygonal cells. These cells, when no longer fresh, or after treatment with various reagents, become opaque, and then, for the first time, it is possible satisfactorily to distinguish their edges, and their central round or oval nuclei. In different animals these cells have different dimensions; in Man they measure about 0.032 mm. (Becker). In the vicinity of the margin of the lens they become for a greater or less distance higher than they are broad, almost cylindrical, and stand perpendicularly to the surface of the lens; further along they become even higher, and pass from the perpendicular to an oblique position, inclining with their inner ends toward the anterior surface of the lens; at the same time they assume a conical form, their broad bases being directed toward the surface of the lens. Farther backwards the cells become still longer, and take a still more oblique direction; their anterior ends bend outwards and advance to meet the ends of the neighboring cells described above. All these relations may be much better understood from the accompanying fig. 337, and plainer yet from fig. 339, which represents the same more highly magnified. In this way, therefore, is effected the junction of the anterior thin layer of the lens-substance with the posterior thicker layer. The transition of the epithelium of the anterior layer into the fibres of the posterior layer takes place, therefore, by a simple lengthening of the former so as to form the latter.

Fig. 337.

Fig. 337. Meridional section through axis of the Human lens.

In successful preparations the epithelial cells in all parts of the anterior layer, and in all the changes which their form undergoes, retain the character of true cells, that is to say, they always possess plainly marked protoplasm and nuclei. Neither myself nor Dr. Sernoff,† who by his researches, under my supervision, has made substantial contributions to our knowledge of the true relations of the structure of the lens, have ever been able in any part of the lens to discover, instead of true cells with well-defined protoplasm and nucleus, "only irregular, sharply contoured nuclei of various size," the so-called formative cells of Becker.

These were described by Becker ‡ as lying very closely together at the point of attachment of the zonula, as having but little protoplasm about them, and often exhibiting distinct cell-division.

* All the drawings have been copied by Sernoff from preparations made by himself.

† *Ueber den mikroscopischen Bau der Linse bei Mensch und Wirbelthieren.* Dissert. inaug. 1867.

‡ *Archiv für Ophthalmologie*, 1863.

The transition of epithelial cells into lens-fibres does not, however, happen in all animals in the manner described. As Heinrich Müller found in Birds and the Chameleon, and as Sernoff and I observed in many of the scaly Amphibia, there exists a modification, consisting in the fact that the flat epithelial cells begin to increase in height only at a short distance from the anterior pole, so as to assume the character of cylindrical cells; they grow gradually longer until they reach the equatorial region, beyond which point they begin again to shorten as they pass backwards, although they do not

Fig. 338.

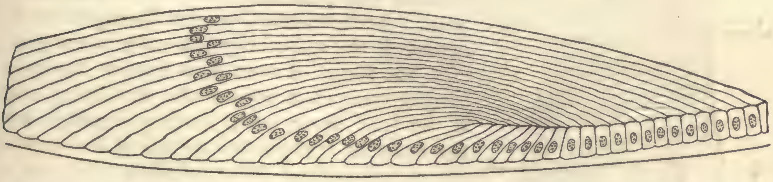

Fig. 338. Meridional section through the border of the lens of the Rabbit, showing the transition of the epithelium into lens-fibres.

again attain the character of flat epithelial cells. These are the perpendicular, radial lens-fibres which were seen in the lens of the Bird by Treviranus and Brücke. All these fibres, or, better expressed, all these lengthened cells appear in sections as more or less regular hexagons; their peripheral ends are broader than the central ones, and in sections generally appear not hexagonal, but rounded. In this end lies generally a single round or oval, sharply contoured nucleus. In the anterior half of the lens these cells are in close apposition by their posterior ends with the inner surface of the capsule; but in the posterior half, almost immediately behind the equator, as Sernoff has demonstrated in Birds, they are separated from the inner surface of the capsule in such a manner as to form around the entire lens a shallow annular canal, which is filled with structureless substance. Exactly such a canal, generally situated posterior to the place where the anterior epithelium is transformed into lens-fibres, has been found by Sernoff and myself, not only in Birds, but also in the embryo of many Mammalians and of Man. It exists in the latter even for some time after birth, while in the Bird it lasts throughout the entire life. While, as stated, the radial cells become shorter in the posterior portion of the lens, they change their direction, so as to take an oblique instead of a radial position, and thus gradually assume the appearance of meridional lens-fibres, like those of the Mammalia. (Fig. 339.)

We shall now consider in what manner the lens-fibres arrange themselves in the construction of the posterior, thicker layer of the lens, which constitutes its most important part. This is accomplished on a plan essentially the same in all the Vertebrates. Flat fibres combine to form curved lamellæ, covering each other like the scales of an onion; these lamellæ at first gradually increase in size as they pass from the point of transition of the epithelial cells into fibres towards the pole of the lens; then they grow smaller in the direction toward the nucleus of the lens, until finally at its centre, or a little posterior to it, they attain their smallest size. Here it should be remarked that the fibres of the first, superficial layers, which form the equatorial portion of the lens, and are therefore situated near the point of transition into epithelium, are curved outwards, that is to say,

their convexity is turned towards the axis of the lens, their anterior ends impinging upon the epithelial layer, while their posterior ends are in immediate contact with the capsule. The fibres of these layers are flatter and smaller in the middle than at their extremities. (Fig. 338.) But the nearer they come to the axis the more the character of their curvature is changed. At first they become straighter, farther inwards s-shaped, until at last they curve in such a way that their ends, the anterior as well as the posterior end, bend towards the pole. At the same time the fibres, while they approach the axis, lengthen only very gradually, the fibres of each next deeper layer projecting somewhat beyond the one lying above it, so that their ends, as they impinge upon the anterior and posterior wall of the capsule, cover one another like roof-tiles.

Fig. 339.

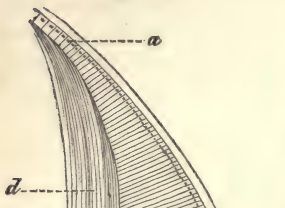

Fig. 339. Similar section from the lens of the Chicken. *a*, epithelial cells; *b*, perpendicular so-called radial fibres; *c*, their transition into meridional fibres; *d*, meridional fibres; *e*, structureless substance; *f*, capsule.

But these relations obtain only in the lens-fibres of certain of the more peripheral layers of the border. The ends of the rest of the fibres, which belong rather to the inner layers of the lens, pass farther on toward the pole and the axis of the lens, and here meet the extremities of those fibres which come from the opposite side. This meeting takes place in different ways in different animals; it is simplest in certain Fish, Amphibia (the Cod Fish—Brewster, Triton—Harting, Salamander—Harley, Frog—Becker), and Birds, in whom the lens-fibres of one and the same layer begin at the equator gradually to diminish in size, and meet each other with pointed ends at a certain point in the axis of the lens, like the interspaces between the meridional lines of the globe. In certain Fish, for instance, in the Torpedo, the posterior ends of the fibres also unite at the axis, while the anterior ends of each layer form, by their meeting, a suture, which by low magnifying powers presents itself upon the anterior surface of the lens as a straight line running at right angles to the axis, and from which the ends of the fibres pass off like radii towards the equator. Since the sutures of the following inner layers also represent straight lines gradually shortening towards the centre of the lens, it may be said that in the given case the anterior ends of the lens-fibres of all the layers meet each other upon a surface (very uneven, it is true), which perhaps takes the form of a triangle, the slightly curved base of which is turned toward the anterior surface of the lens, while its apex is lost in its nucleus.

In the greater proportion of Fishes and Amphibia and some Mammalia (the Rabbit, Hare, Dolphin) the anterior as well as the posterior ends of the lens-fibres terminate in the manner described, so that the posterior and anterior sutures, which have the appearance of straight lines, do not lie in the same plane, but cross each other at right angles. In this case the fibres do not pass around the entire half of the lens, but only a portion of it, and this

happens as follows:—If, for instance, the anterior end of a fibre begins at the end of the anterior suture, it ends, passing backwards in a meridional direction, in the middle of the posterior suture, and consequently in the axis of the lens. If a fibre begins in the middle of the anterior suture it terminates at the end of the posterior suture. In the Human fœtus, in the newly born, and in many, perhaps in the majority of animals, the junction of the fibres on the anterior as well as the posterior surface of the lens displays a complicated arrangement as follows: The sutures form a sort of star, containing three principal radii, whose point of union corresponds to the axis of the lens. The angle thus formed by any two of these radii equals 120°. The radii of the anterior and posterior star do not lie in the same plane, but are arranged in such a way that the plane of each anterior radius falls half way between two radii of the posterior star; in other words, the anterior and posterior stars are twisted one upon the other at an angle of 60°. Finally, there are animals in whom, as also in the Human adult, the stars consist of a greater number of radii. Thus, for example, in Man we may count as many as nine radii in the anterior star, and in the posterior star even more. (Figs. 340 and 341.) Not infrequently the radii divide at their ends, but even with this complication the radii of the anterior and posterior stars do not lie in the same plane. Moreover, this complication affects only the most superficial layers of the lens, since in the deeper layers these compound stars, as has been observed in the lens of the full-grown Man, transform themselves into stars with three radii.

Fig. 340.

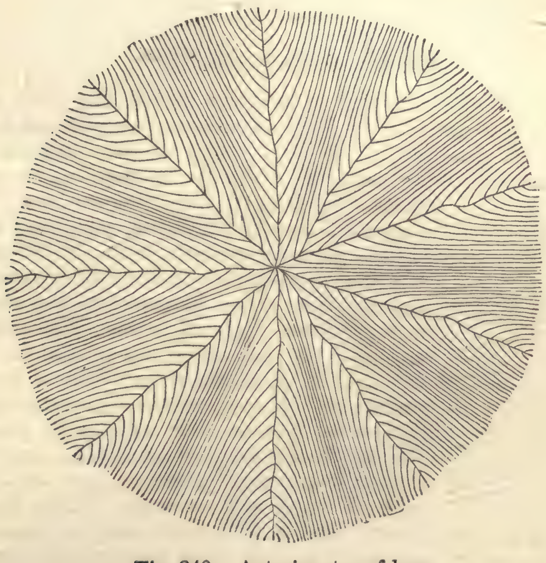

Fig. 340. Anterior star of lens.

All former investigators (Werneck, Hannover, Kölliker, Henle, Leidig, Becker and others) thought that the ends of the fibres did not come into immediate contact with one another at the radii of the star, but that between them there was an interspace filled with a structureless or granular substance, and this was considered to be a constant element of the lens.

Since now the stars pass through all the layers of the lens, therefore it was supposed that there must be fissures corresponding to the rays of these stars, and penetrating from both anterior and posterior surface towards the nucleus of the lens. Becker (*Archiv für Ophthalmologie*, 1863) ascribed to

Fig. 341.

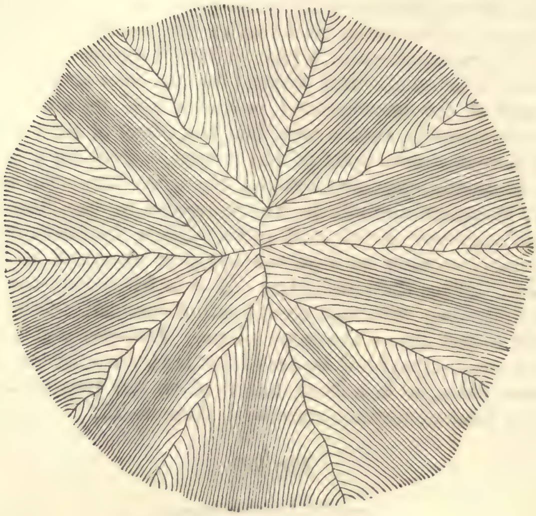

Fig. 341. Posterior star of lens.

these fissures—which, according to him, are during life filled with a semifluid, perfectly homogeneous, transparent substance—a special importance in the physiological function of the lens. He, in fact, believed that these fissures communicated by means of openings in their walls with special canals, which spread out between the fibres of the crystalline lens (interfibrillar passages), so that during the changes incident to the act of accommodation the contents of the stellate fissures might be emptied into these passages, or the reverse. But even Kölliker declared in his *Microscopical Anatomy* (p. 711) that, where the ends of the fibres were well preserved, he found very little of the substance mentioned. Hensen affirmed that the passages described by Becker were artificially produced, and Sernoff finally demonstrated that neither stellate fissures with their contents, nor the interfibrillar passages have any existence. The latter author showed that in quite fresh and well-hardened preparations the lens-fibres impinge directly upon one another at the rays, and that the rays themselves, when viewed with high magnifying powers, appear as undulating lines. (Fig. 342.) Carefully-made sections of the lens in any direction show likewise that between its fibres no interspaces exist. It is thus demonstrated that the structureless substance as well as the inter

Fig. 342.

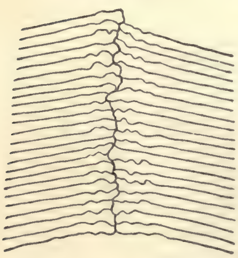

Fig. 342. Horizontal section through a suture of the lens of the Ox, showing the manner in which the lens-fibres at this point impinge upon one another.

fibrillar passages described by Becker are nothing more than artificial products, the former of which obviously depends upon a degeneration of the ends of the lens-fibres, while the latter are caused by careless and roughly made sections with consequent displacement of the fibres.

With regard to the lens-fibres we know that their length, thickness, etc., differ in the different layers; nevertheless they always retain the character of flat bands, which in sections present themselves as larger or smaller elongated octagons. If the section passes through several fibres in their natural position, we shall have a figure which reminds us of the honey-comb, whose cells are drawn out in one and the same direction parallel to the surface of the lens. (Figs. 343 and 344.) From this transverse section we may see how the border of one fibre is inserted into the angle formed by the borders of the neighboring, adjacent fibres. In Birds these octagons are very long and narrow, which shows that in them the fibres are much flatter than in the Mammalia. (I refer the so-called radial fibres in Birds to the anterior epithelial layer of the lens.) In Fish the fibres are so flat that it is difficult to say with certainty what form they possess in transverse sections.

Fig. 343.

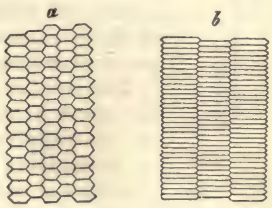

Fig. 343. Perpendicular section through lens-fibres in their natural position. *a*, from the Calf; *b*, from the Chicken.

In general the most superficial lens-fibres are broader and thicker than those which are more deeply situated. Also the dimensions of the same fibres in transverse sections are not everywhere the same. In Man those fibres which lie at the border of the lens, and which, as above stated, are curved outward, are thicker at their ends than in the middle. Those fibres on the other hand which lie nearer to the nucleus, and whose ends bend toward the axis of the lens, gradually taper off from the centre; their ends, however, become somewhat broader again. In the Mammalia the greater portion of the lens-fibres terminate at some point on the surface or at the rays of the star in thickened or expanded ends. If the lens-fibres reach the axis (as is the case, according to the above, with certain Fishes, Amphibia, and Birds), or if they meet each other only in one line (as in the Rabbit, Hare, etc.), it is obvious that their ends do not expand, but gradually grow smaller from the equatorial region and terminate in the first case quite pointedly, and in the second case more or less obtusely.

The contours of the fibres are likewise diverse. In all animals the superficial fibres always have smooth, and the deeper ones uneven and even serrated edges. This is least frequently the case in Man, and occurs in preference at the ends of the fibres. The serration is more pronounced even in the Mammalia, and still more in the Amphibia and in Birds. In the majority of Fishes the fibres, as Brewster indeed showed, are beset with very long and regular teeth. (Fig. 344.) However long the teeth may be, they diminish in length toward the ends of the fibres, and finally become only wavy inequalities. The teeth of one fibre are directed toward the teeth of the adjacent fibres, and possibly under some circumstances interlock with them; this is decidedly not the case in the Mammalia and in Birds.

Those fibres which are situated immediately upon the border of the lens, and for a certain distance inwards, all possess a single, sharply contoured, oval nucleus, in the centre of which a round nucleolus may be seen. These

nuclei are differently situated in different fibres. In the neighboring fibres, however, they are not far separated from one another, so that in meridional sections of the lens they form a more or less broad and variously curved belt, the so-called nuclear zone of Meyer, which proves to be an immediate continuation of a regular row of epithelial nuclei. (Figs. 338 and 339.)

Fig. 344.

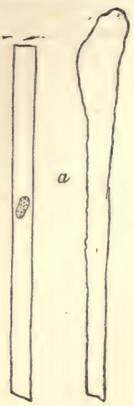

Fig. 344. Isolated lens-fibres. *A*, from Man; *B*, from the Fish; *a*, middle portion; *b*, end.

Ritter (*Archiv für Ophth.*, Bd. xii., Abth. 1, p. 17) discovered in the centre of the lens of the Frog short fibres with nuclei, or, more properly speaking, cells which, in his opinion, represented the formative elements of the lens-fibres. Sernoff found similar cells, but in the Frog only. If we bear in mind that these cells are very resistant, that their surface is generally very irregular and wrinkled, that nuclei are not always found in them, or when found present an irregularly serrated appearance, it seems much more reasonable to consider them as the remains of old embryonal cells, which have reached only a certain stage of development, rather than as young formative cells or productive material of the lens-fibres.

The consistence of the lens-fibres varies according to the layers in which they are found. The superficial fibres are generally very soft and delicate, and are easily resolved by macerating fluids into separate drops of various size (vitreous globules), and partly also into a finely granular, structureless mass. This resolution occurs also spontaneously after the death of the animal. Since this degenerative process attacks at first the extremities of the fibres, it is plain that its products must collect first of all at the lens-star; these products were formerly held for normal elements of the lens. Moreover, under certain conditions vacuoles occur in the fibres; often under such circumstances their borders appear as it were gnawed out. The deeper and the nearer the centre the fibres lie, the more resistant are they, and the less easily affected by reagents.

The authors generally assign to the lens-fibres a sheath, and therefore describe them by another name, namely, as the tubes of the lens. But it is exceedingly difficult to prove the presence of a sheath, especially in the exceedingly thin, serrated fibres of the Fish, and the grounds upon which the authors rely are even less tenable than those which favor the existence of a membrane on the blood-globules. Longitudinal and transverse striæ are also described as existing in the lens-fibres. But this striation is so seldom observed, and presents so many irregularities and inconsistencies in its arrangement, that we are not justified in regarding its presence as an indication of the minute internal structure of the lens-fibres; this must rather be considered as an accidental wrinkling and irregularity of the fibres.

Under the influence of dilute mineral acids, alcohol, and by cooking, the fibres of the lens become opaque, and their contours at the same time become more sharply defined. This depends upon the fact that albumen forms one of their most important elementary parts, namely, in a preponderating mass of globulin, with a certain amount of albuminate of potash and the ordinary albumen of serum. Moreover, among the ingredients of the lens-fibres there is some fatty matter with traces of cholesterin, 60 per cent. of water, and not more than $\frac{1}{2}$ per cent. of salts. The qualitative conditions must change according to the layers to which the fibres belong; for aside from the fact that the central fibres are more resistant, the nucleus of the lens

becomes much harder by the action of reagents than the superficial layers, so that in the Fish, for example, the nucleus remains transparent, becoming at the same time hard, and difficult to cut. The cloudiness and formation of vacuoles in the lens-fibres is also caused by agents which deprive them of water.

In regard to the origin of the body of the lens and the formation of the fibres composing it, it is plainly to be inferred from the above described direct transition of the anterior epithelial layer into the posterior fibrillar layer, that each lens-fibre is nothing but a colossal, elongated, epithelial cell; the history of development also teaches that the elements of the lens substance arise from the epidermoid or external layer of the embryo.

As mentioned above, the body of the lens is surrounded on all sides by a membrane, which is completely structureless, smooth, and transparent. Only in cases where this membrane is very thick is it possible in transverse sections of hardened preparations to recognize a longitudinal striation, which points toward a division into layers. The capsule is not everywhere equally thick. The anterior half, and especially that portion which is adjacent to the point of attachment of the zonula Zinnii, is always thicker (in Man nearly twice as thick) than the posterior half. It is thinnest at the posterior pole. The substance of the capsule is quite resistant and very elastic. When incised it readily rolls itself outwards. Some authors have found epithelial cells upon the posterior surface of the capsule, which probably arose from the fact that the inner surface of the anterior capsule was considered and described as covered with epithelial cells. But it would be more natural, in view of the mode of development of the lens, to take a reversed view of the matter, namely, to consider that the epithelium, which forms the anterior layer, and is the direct continuation of the posterior layer, is, like the latter, also covered by the capsule. It would seem that either the impress of the posterior ends of those fibres which impinge directly upon the capsule, or the globular structures which are formed by the disintegration of these ends, had been taken for epithelial cells. The question as to the genetic signification of the capsule of the lens offers the greatest difficulties in its solution. It is said indeed that it is the product of secretion of the epithelial cells as well as of the lens-fibres, but there is no proof whatever of this position. I have very often noticed that the first foundation of the capsule, which is exceedingly delicate, was folded and separated from the surface of the embryonal lens, a state of affairs which poorly coincides with the idea of its being a product of secretion. I have had the opportunity of seeing (in the embryo of the Chicken) in preparations made by Sernoff, who occupied himself for a long time with this question, that the capsule of the lens contained nuclei, and it would perhaps be more natural to reckon it among the metamorphosed structures of the connective tissue. The question, however, has obviously not as yet been brought to a conclusion.

VII. THE CORNEA.

By ALEXANDER ROLLETT.

THE cornea of the eye of vertebrate animals consists of several layers of different kinds of tissues. The anterior and posterior limits of the layers run nearly parallel to the surfaces of the cornea; they are bounded laterally at the margin of the cornea (limbus corneæ) by the conjunctiva, the sclerotica, and the ligamentum pectinatum iridis.

Layers of the Cornea. (Fig. 345.)

The tissues of the cornea are arranged in layers, counting from without inwards as follows:—

1. The external epithelium of the cornea, fig. 345, *a*—*b*. This is a laminated, flat epithelium.

2. The true corneal tissue (substantia propria seu fibrosa corneæ, fibrous layer of the cornea, lamellated cornea), fig. 345, *b*—*c*. With this layer begin those layers of the cornea which belong to the tissues of the connective substance.

3. The membrane of Descemet (membrane of Demours, membrana humoris aquei, vitreous lamella of the cornea, lamina elastica posterior—Bowman, internal basement membrane—Henle, fig. 345, *c*—*d*). A sharply defined, in general homogeneous appearing membrane.

4. The endothelium of the membrane of Descemet (internal epithelium of the cornea, epithelium of the membrane of Descemet, epithelium humoris aquei, fig. 345, *d*—*e*), a simple layer of flattened cells.

Sections perpendicular to the surface of the cornea, which has been hardened in either chromic acid, Müller's fluid, or alcohol, or dried or frozen, exhibit distinctly the arrangement in layers described above. The layers are of different thickness, the thickest being that formed by the true corneal tissue; this is in Man about one mm. in thickness at the periphery, in the centre it is somewhat thinner (Brücke).* Next to this layer in thickness comes the external epithelium, which in Man is 0.03 mm. thick (Henle).† Then comes the membrane of Descemet, in the adult 0.006—0.008 mm. in the middle, and at the border 0.01—0.012 mm. in thickness (H. Müller); ‡ last of all is the endothelium of the membrane of Descemet.

The picture presented in such sections by the external epithelium, the membrane of Descemet, and its endothelium needs no further preliminary explanation (fig. 345); the appearances presented by sections of the true corneal tissue, however, are not so easily understood.

If, for example, we take a section, colored with carmine, from an eye hardened in Müller's fluid (fig. 345, *b*—*c*), this layer presents a band-like appearance. The substance which forms the groundwork appears by no means regular, being divided into stripes (lamellæ, lamellæ of Bowman), or secondary lamellæ (Henle),§ which take a longitudinal course parallel to the surface of the cornea; this division is accomplished by means of elongated figures taking the same direction, and being in some places

* *Anat. Beschreibung d. menschl. Augapfels.* Berlin, 1847, p. 9.
† *Eingeweidelehre.* Braunschweig, 1866, p. 605.
‡ *Archiv für Ophth.* Bd. ii., 1. Abth., p. 48.
§ L. c., p. 605.

broader and in some places narrowed down to simple lines. The broader portions taper off and become continuous with the lines, which either serve as connecting links with the broader portions, or are gradually lost in the corneal substance. Within the dilated portions lie elongated masses which seem to be darker and more highly colored than the groundwork. These

Fig. 345.

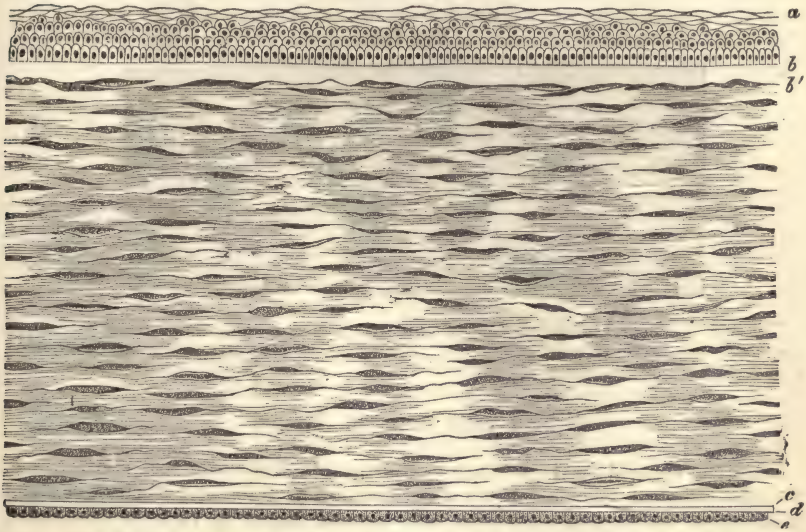

Fig. 345. Meridional section through the cornea of the Human adult, from an eye hardened in Müller's fluid. The section was colored with carmine, and made transparent by the oil of cloves.

masses (the corneal corpuscles of Toynbee and Virchow) either completely fill the fissures in the groundwork, or, as in other places, are on one or both sides separated from the groundwork, being smaller than the deficiencies in the corneal substance. At a certain distance from the external epithelium and not far from the external surface of the cornea (fig. 345), these broader figures lie more closely together than in the other portions of the section; and between this layer and the external epithelium lies a band of corneal substance which is broader than all the others (lamina elastica anterior—Bowman, anterior basement membrane—Henle),* fig. 345, *b*—*b′*. This reminds, by its equable, smooth appearance, of the membrane of Descemet, but is broader and never so sharply defined as that. Towards the epithelium its marginal contour is not so distinct as that of the membrane of Descemet toward the internal epithelium. The inner border of this band is still less sharp, since it gradually passes over into the bridges of corneal substance left between the corpuscles. The condition described is very distinctly to be seen in sections through the central portions of the Human cornea. In the marginal portions the appearance is somewhat different, since in this region bands similar to those of the corneal substance pass from the deeper layers to the edge of the epithelium and thence return again (fibræ arcuatæ), the so-called supporting fibres (Henle).* In some animals, in the Ox, for instance, this arrangement, is the rule in all parts of the cornea.

* L. c., p. 605.

In the thin corneæ of small animals, for instance, in the cornea of the Frog, we may observe the arrangement of the layers by placing under the microscope the cornea, which has been cut out with a pair of sharp scissors and immersed in humor aqueous, and examining those places where the membrane has been thrown into folds. In this connection see fig. 346.

These layers of the cornea must now be examined more closely with reference to their minute structure.

Fig. 346.

Fig. 346. Corneal layers in a fold of the Frog's cornea, examined fresh in humor aqueous. *ab*, external epithelium; *bc*, corneal tissue; *d*, membrane of Descemet; *e*, endothelium of the latter.

The true Corneal Tissue.

The true corneal tissue belongs to the tissues of the connective substance. As microscopical forms of it we may distinguish cells, and fibrils arranged in bundles, which latter traverse the corneal tissue in various directions, and finally peculiarly-shaped cavities which contain the corneal cells. In the corneal tissue, therefore, we find forms not unlike those of the fibrillar connective tissue, with which the true corneal tissue possesses many similarities; these two tissues also present a very similar and nearly related history of development.*

The cells of the corneal tissue. We distinguish in the corneal tissue two different forms of cells.

Toynbee† gave the first but little-noticed description of one form of cells, but Virchow, incidental to his studies‡ on the connective substances, brought them so forcibly to notice, that since that time, under the name of corneal corpuscles or corneal corpuscles of Toynbee or Virchow, they have afforded even to our own day a rich theme for the studies and disputes of histologists. Von Recklinghausen§ first called attention to the second form of cells in the corneal tissue. This latter form will be considered by us first.

Wandering cells, and infiltration of the cornea with wandering cells. The wandering cells (movable cells of the cornea, V. Recklinghausen)‖ are to be recognized in the living tissue by their active amöboid movements.¶

They are easily to be found in any freshly extirpated Frog's cornea which

* Compare this handbook, pp. 53—56, and pp. 67—68.

† *Philosoph. Transactions*, 1841, Part ii. p. 179.

‡ *Würzburger Verhandlungen.* Bd. ii., pp. 154 and 314. *Cellularpathologie.* Strube, *Der normale Bau der Hornhaut u. die pathol. Abweichungen in demselben, Diss. inaug. Würzburg*, 1851.

§ "Ueber Eiter- und Bindegewebskörperchen." Virchow's *Archiv*, Bd. 28, p. 157.

‖ L. c., p. 168.

¶ Compare this handbook, pp. 57 and 58.

is placed under the microscope in a moist chamber, with the addition of a little humor aqueous, and with the membrane of Descemet upwards (v. Recklinghausen, Engelmann).*

Their number varies in different corneæ. They appear more distinct and sharply defined after the preparation has stood for some time, and then they attract attention by their lustre. Their active changes in form resemble perfectly those of the amöboid cells of the Frog's blood, or of the pus corpuscles found in the humor aqueous of the same animal. In the corneal tissue, however, their forms are often markedly lengthened, and also very small. The movable cells wander about in the tissue. This phenomenon can only be understood when we take into consideration not only the mobility of the cells, but also the penetrability of the medium (the corneal tissue) in which we observe them. Reserving the latter consideration for a future time, let us take for granted the penetrability of the tissue and follow the cells independently.

Wandering cells are to be found throughout the whole corneal tissue. The paths which they follow are various, but generally strongly curved (v. Recklinghausen).† Nevertheless they may also take a straight course. In the latter case the transit of a cell through the field of a Kellner's microscope occupies from half an hour to an hour (v. Recklinghausen). The wandering cells are to be observed in the fresh corneæ of other animals as well as in the Frog.

Among the Mammalia, observations on this point have been made on the Rat, the Rabbit, the Dog, the Sheep, the Ox, and the Pig (v. Recklinghausen). But for this purpose it is necessary to make thin sections of the thicker corneæ with a sharp knife. The wanderings are often quite as well marked as in the Frog, although not in every case.

The wandering cells of the Frog's cornea are changed into roundish, highly refractive bodies, with short processes or off-shoots, when the cornea is immersed in a moderately strong solution of sugar (v. Recklinghausen, Engelmann). The number of the wandering cells increases considerably, if inflammation be excited by cauterization with nitrate of silver (purulent infiltration). The case is the same in every traumatic keratitis excited by other means.

After in the first place the amöboid character of the pus-cells, which appear in the humor aqueous after inflammation of the cornea, had been established, and also the earlier views, defended by Virchow, concerning the identity of the pus corpuscles with the white-blood corpuscles had been already set forth, it instantly became known that the pus-corpuscles in purulent infiltration of the cornea possess the same capability of motion, and that similar amöboid cells, although few in number, occur in the normal cornea as wandering cells (v. Recklinghausen).‡

In the study of the cornea we cannot avoid a closer inquiry into the origin of the amöboid cells which make their appearance in purulent infiltration; and for the reason that, as we shall hereafter see, the studies on this subject take a decided part in the controversies on the character and signification of those cell-forms in the cornea, which were formerly designated by the name corneal corpuscles, or corneal corpuscles of Toynbee or Virchow.

In the first place attention was drawn to appearances which gave rise to the opinion that the opacity of the cornea in traumatic inflammation was due to a proliferation of the cells (nuclei) contained in the cornea (Bowman).§

When the corneal corpuscles began to be more carefully examined, their changes

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* *Ueber die Hornhaut des Auges*, Leipzig, 1867, p. 3.

† L. c., p. 171.

‡ L. c., p. 157—171.

§ *Lectures on the Parts concerned in the Operations on the Eye, and on the Structure of the Retina.* London, 1849, p. 29, fig. 5.

in inflammation became the subject of investigation (Virchow,* Strube),† and the attempt was made by prolonged studies in this direction (His,‡ Weber,§ Rindfleisch,‖ Langhanns)¶ to give a more definite form to the idea of the derivation of pus corpuscles from the corneal corpuscles. Finally, after the recognition of the amöboid character of the wandering cells, it was suggested how the corneal corpuscles, either directly or by consequent cell-division, might be transformed into wandering cells (v. Recklinghausen).** But at the same time it was also ascertained that corneæ which had been extirpated from various animals, and which while still living, or after previous death, had been preserved in the lymph-sacs of the living Frog, absorbed at their margins numerous amöboid cells from the neighboring tissues (v. Recklinghausen).††

And only a few years later the theory was broached that the pus corpuscles of Keratitis in the living animal, as well as of inflammation in other organs, should be considered for the most part as white blood corpuscles, that had emigrated and wandered into the tissue of the cornea (Cohnheim).‡‡ This, as soon appeared, was a return to forgotten ideas, which had long ago been proposed on the ground of direct observation upon the subject of the formation of pus (Waller).§§ These observations related primarily to the ability of the blood corpuscles to pass through the walls of the vessels; an occurrence which has only been demonstrated in a satisfactory way by recent direct observations on the passage of red (Stricker)‖‖ and white blood corpuscles (Cohnheim)¶¶ through the walls of the vessels.

The origin of the numerous pus corpuscles which make their appearance in purulent infiltration of the cornea should therefore, it was said, be sought only in the blood and not in the corneal corpuscles, since the latter remain entirely unchanged in the infiltrated portions of the cornea (Cohnheim). Moreover the purulent infiltration was said always to begin at the margin of the cornea, at that portion therefore which, as we shall hereafter see, is furnished with vessels; and granular pigments (anilin blue, vermilion) which had been introduced into the circulation at some remote point reappeared in the pus corpuscles of the cornea (Cohnheim).***

In contradiction to this opinion it has been proved that, in a breeding chamber constructed by v. Recklinghausen, a collection of movable cells made their appearance around the irritated spot, even in the corneæ of Mammalia and Frogs which had been cut out and cauterized. But these cells should be considered as the genetic successors of the simultaneously disappearing corneal corpuscles (F. A. Hoffmann).††† The opacity commencing at the margin of the living cornea which has been cauterized (His, Cohnheim) should certainly be considered as due to wandering cells from the blood, but the opacity around the point of irritation should be attributed to this proliferation of the corneal corpuscles (F. A. Hoffmann).‡‡‡

On the other hand it was claimed in favor of the non-participation of the corneal corpuscles in the formation of pus, that no opacity appeared in the Frog's cornea after cauterization, if the blood of the animal had previously been (as Cohnheim imagines) entirely displaced by a 0.75 per cent. solution of common salt injected through the vena abdominalis for one to two hours. This would speak decidedly for a non-participation of the corneal corpuscles in the formation of pus (Cohnheim).§§§

Shortly after this, however, new researches were published (Norris and Stricker),‖‖‖

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* "Ueber parenchymatöse Entzündung." Virchow's *Archiv*, Bd. iv., p. 259.

† L. c.

‡ *Beiträge zur norm. und path. Histologie der Hornhaut.* Basel, 1856, p. 45.

§ "Zur Entwickelungsgeschichte des Eiters." Virchow's *Archiv*, Bd. xv., p. 475.

‖ "Untersuchungen über die Entstehung des Eiters." Virchow's *Archiv*, Bd. xvii., p. 239.

¶ "Das Gewebe der Hornhaut im normalen und patholog. Zustande." *Zeitschr. für rat. Med.* 3 Reihe. Bd. xii., p. 22.

** L. c., p. 181.

†† L. c., p. 183.

‡‡ "Ueber Entzündung und Eiterung." Virchow's *Archiv*, Bd. xl., p. 1.

§§ *Philosophical Magazine*, 1846. Tome 29, pp. 271 and 398.

‖‖ *Sitzungsberichte der Wiener Akademie.* Bd. 52, p. 379.

¶¶ L. c., p. 38.

*** L. c.

††† "Ueber Eiterbildung in der Cornea." Virchow's *Archiv*, Bd. 42, p. 204.

‡‡‡ L. c., pp. 209—217.

§§§ "Ueber das Verhalten der fixen Bindegewebskörperchen bei der Entzündung." Virchow's *Archiv*, Bd. xlv., p. 333.

‖‖‖ *Studien aus dem Institute für experimentelle Pathologie in Wien.* Herausgegeben Von Stricker, 1870, pp. 1, 18, and 31.

in which the proliferation of the corneal corpuscles in inflammation, and the transformation of the same into wandering cells, are most conclusively maintained, and illustrated by a number of drawings.

There are, therefore, according to the various authors, two distinct sources of origin for the wandering cells of the cornea, and these are claimed in different ways: the blood alone, the corneal corpuscles alone, or both together.

We shall take up these questions again, after we have first become better acquainted with the characters and appearances of the second form of corneal cells.

The cellular network of the cornea. The corneal corpuscles. Corneal corpuscles of Toynbee or Virchow. Stellate (radiating) *corneal corpuscles. Immovable corneal corpuscles* (v. Recklinghausen).* *Fixed corneal corpuscles* (Cohnheim). These structures present for our consideration nucleated cells devoid of a membrane. Each cell possesses a flat body and a similarly shaped nucleus; the small diameter of the cell stands perpendicularly to the surface of the cornea, or deviates but little from this direction. The flat surface of the cell therefore presents itself if we view it perpendicularly to the surface of the cornea, or observe, under the microscope, sections parallel to the surface. The edge of the flat cell then appears irregular, since from it a greater or less number of processes pass off in every direction.

These processes divide into branches, at the same time diminishing in size; they do not meanwhile remain in the same plane with the flat body of the cell, but deviate from it above or below. The processes arising from the neighboring cells also unite with one another, so as to form a cellular network which traverses the whole cornea. The meshes of this network are of various form; not infrequently the frame-work formed by the processes of the cells appears regularly rectangular. The substance of the cells and that of their processes have always the same appearance, often smooth and homogeneous, often finely granular.

The preceding general description of the cellular network formed in the corneal tissue by the corneal corpuscles corresponds to a definite condition of the cells, and is repeated in the corneæ of the most different animals (the Frog, Triton, Dog, Cat, Ox, Rabbit, Guinea-pig, Pig, Sheep, Hedgehog, Bat, Rat, Mouse, Fox), and of Man in an exactly similar manner.

In respect to the form and arrangement of the cells and their processes, this description of the corneal corpuscles agrees with that which has prevailed since His † described the beautiful pictures obtained from preparations made with pyroligneous acid. In respect to the character of the cells and processes, formed and arranged as above described, we have expressed our opinion in conformity with the recent views concerning the cell-theory. While immediately after the above-mentioned work of His, many histologists with him considered the cellular network as hollow, the cells and their processes being provided with membranes, after the manner of the plasmatic network ascribed by Virchow to the tissues of the connective substance, we recognize it as a protoplasmic network (Kühne) spreading throughout the entire cornea.

This opinion, however, is not undisputed. The cellular network of the stellate corneal corpuscles has also been affirmed to be an artificial product. It has been held that in point of fact the corneal cells would seem rather

* L. c., p. 180.
† *Würzb. Verhandl.*, Bd. iv., p. 90.

to be transparent plates of elastic nature, with oval, elongated, or irregularly indented single or seldom doubled nuclei. These cell-plates would then resemble endothelial cells; and since flat nucleated cells have been demonstrated in the tendons (by Ranvier),* the opinion might gain ground that flat cells arranged in rows in the connective tissue play a more or less exclusive (?) rôle (Schweigger-Seidel).†

Our examination of the corneal corpuscles will lead us to the conclusion that this theory of elastic cell-plates cannot be maintained in opposition to the old idea of branched corneal corpuscles combining to form a network. Let us now undertake the examination of these cells in the living tissue (v. Recklinghausen,‡ Kühne,§ Engelmann).‖

If we place under the microscope a living cornea which has been rapidly excised with a small border of the adjacent sclera, and moisten it with humor aqueus, it will at first present an appearance as homogeneous as that of the perfectly transparent, clear, fresh cornea (Engelmann,¶ Stricker);** only where folds and wrinkles exist the picture represented in fig. 347 will soon be developed (Engelmann).

After a time the wandering cells first make their appearance, and soon the corneal corpuscles also, at first as dull stars (v. Recklinghausen,†† Engelmann),‡‡ or as spindle-shaped figures (Kühne),§§ in which neither granules nor nuclei are to be seen.

Sooner or later, however, small granules and the generally elongated nuclei become visible, and the corneal corpuscles are, in consequence, more distinct. The close conformity of the index of refraction in all portions of the fresh cornea is therefore gradually lost in the excised cornea. At first it is only with difficulty and in certain parts that the corneal corpuscles may be followed; afterward the task becomes more and more easy. The Frog's cornea, removed from an eye which has been kept for some time in a moist atmosphere, is particularly suited for the demonstration of the corneal corpuscles (Kühne).‖‖

If the excised cornea of the Frog be preserved for twenty-four hours in the sac of the Frog's nictitating membrane (Stricker),¶¶ we shall have the appearances represented in fig. 347.

In this case it is easy, by adjusting the focus, to follow the network formed by the corpuscles throughout the whole cornea.

The chloride of gold (Cohnheim)*** is a very excellent agent for displaying the cellular network of the cornea. The fresh cornea of the Frog immersed in a 0.5 per cent. solution until it becomes yellow throughout, and then exposed in water, with a few drops of acetic acid, to the action of light, soon acquires a reddish or bluish color; a cornea thus treated, and after several days examined under the microscope in glycerine, the anterior epithelium having been brushed off, presents one of the most beautiful pictures, in so far as regards the completeness and distinctness of the cellular network, which is colored red or blue by the reduced gold (fig. 348, *a*).

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* *Archives de Physiologie, normale et pathologique.*

† "Ueber die Grundsubstanz und die Zellen der Hornhaut des Auges." *Sitzungsberichte der k. sächsischen Gesellschaft der Wissenschaften.* Math.-Phys. Classe 1869, pp. 320—323, and 328.

‡ L. c., p. 171, Taf. ii., fig. 2.

§ *Untersuch. über das Protoplasma und die Contractilität.* Leipzig, 1864, pp. 123-131.

‖ L. c., pp. 3 and 4.

¶ L. c., p. 4.

** L. c., p. 1.

†† L. c., p. 171.

‡‡ L. c., p. 5.

§§ *Untersuchungen über das Protoplasma und die Contractilität.* Leipzig, 1864, pp. 124 and 125.

‖‖ Pp. 130 and 131.

¶¶ L. c., p. 36.

*** Virchow's *Archiv*, Bd. 38, pp. 346–349.

Thin sections may be made of corneæ thus prepared, perpendicular to the surface. Such sections are worthy of examination, as showing the course of the processes of the corneal corpuscles. These processes are to be seen traversing the corneal substance in all directions; when cut longitudi-

Fig. 347.

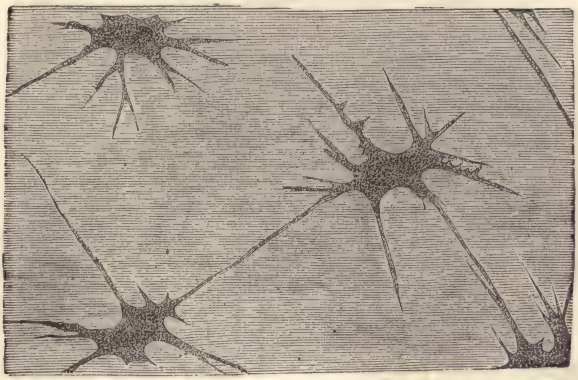

Fig. 347. Corneal corpuscles from the Frog's cornea, freshly extirpated, and preserved for twenty-four hours in the sac of the membrana nictitans. Only the corneal corpuscles and processes of a single plane are represented.

nally, they appear to be in connection with the nucleated centre of the cell. In such preparations we may find, however, oblique and transverse as well as longitudinal sections of the processes (fig. 348 *b*).

It is also very instructive to pick to pieces sections both parallel and perpendicular to the surface of the corneæ thus prepared, and to observe the relations of the cells and their processes; such a procedure is necessary to the study, hereafter to be considered, of the relations of the cells to the basis-substance of the cornea.

Successful preparations, by the chloride of gold, of the corneæ of the most diverse animals present appearances essentially corresponding to the cellular network of the Frog's cornea; a fact which is important in so far that in the cornea of the Frog we have the best opportunity of convincing ourselves that the gold renders the corneal corpuscles visible in a precisely similar way with various other methods, with the exception that it colors them. It is to be remarked that the cell-substance surrounding the nucleus corresponds exactly in appearance with the substance of the processes, in the gold preparations, just as in the methods of preparation which have been already mentioned.

We possess also other methods of impregnating the cornea with metallic salts, such as the treatment with nitrate of silver (Coccius,* His,† v. Recklinghausen);‡ also the impregnation with iron, lead, the salts of copper, with subsequent treatment with SH and NH_4S, ferrocyanide of potash, etc. (Leber).§ These methods also give us a view of the above-mentioned

* M. C. A. Flinzer. *De argent. nitric. usu et effectu*, etc. Leipzig, 1844.

† L. c., p. 67.—Virchow's *Archiv*, Bd. 20, p. 207.—*Schweizerische Zeitschr. für Heilkunde*, 2 Band. No. 1.

‡ Virchow's *Archiv*, Bd. 19, p. 451.—*Die Lymphgefässe und ihre Beziehung zum Bindegewebe.* Berlin, 1862, p. 4.

§ "Zur Kenntniss der Impregnationsmethoden der Hornhaut und ähnlicher Gewebe." *Archiv für Ophth.*, Bd. xiv., pp. 300–316.

protoplasmic network, but they can only be properly understood when at the same time the medium in which the cells are embedded (the basis-substance) is taken into consideration; and therefore we shall take up this subject hereafter.

Fig. 348.

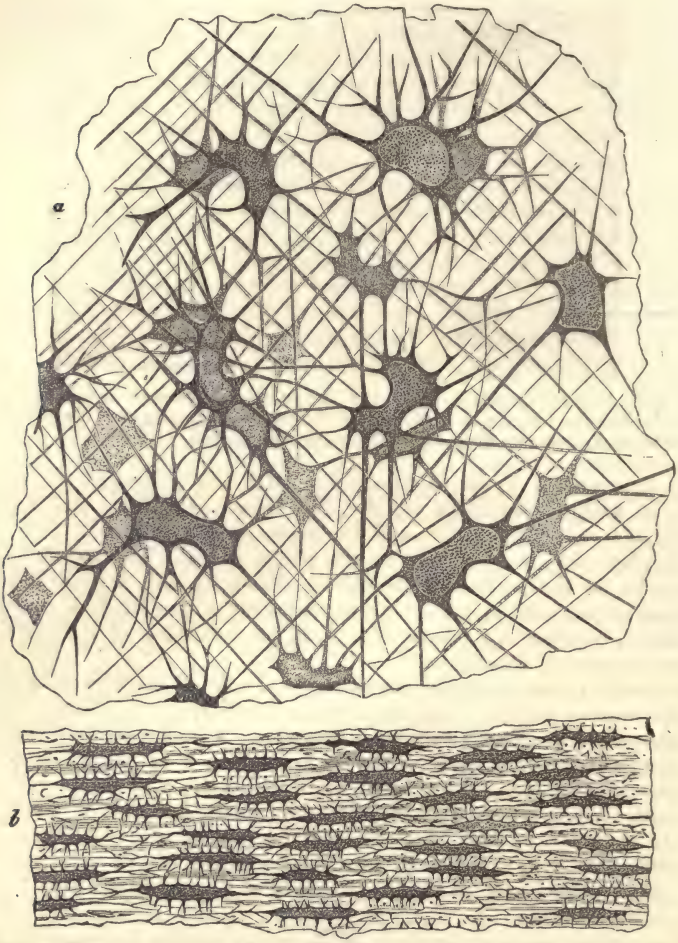

Fig. 348. *a*, Corneal corpuscles from a Frog's cornea treated with chloride of gold, viewed from the surface; *b*, corneal corpuscles from a section perpendicular to the surface of the same.

The chloride of gold, as appears from the foregoing, deserves the fullest recognition as reagent on the corneal corpuscles; nevertheless I must here recommend also another method: it consists in exposing the cornea, immersed in humor aqueus in a simple chamber,* to the action of iodized vapor. In the iodine-chamber the cornea takes a brown color, and the epithelium is

* Described by myself in *Den Untersuchungen aus dem Institute für Physiol. und Histol. in Graz.*, Leipzig, 1870, pp. 15 and 18.

easily detached. If this is removed and the preparation replaced, if necessary, in the iodine-chamber, the cellular network of the cornea may be seen to present itself with a distinctness but little inferior to that of the gold preparations. Also the wandering cells become plainly visible by their beautiful brown coloring. The absorption of the iodine proceeds very rapidly and its working may be followed under the microscope; this method is absolutely certain for the fixing of temporary conditions of the cornea, and for this purpose it cannot be too highly recommended. Whoever works with the chloride of gold will see that, however beautiful the successful preparations may be, there is something uncertain about it, so that often with the most careful procedure the preparations either wholly or in part fail, and this in certain studies is a very unpleasant accident. Not only is the iodine-vapor admirably adapted for the exhibition of the cellular network, and not only can we assure ourselves step by step with regard to the significance of the iodine reaction in the exhibition of cells, by corroborative experiments on fresh masses of protoplasm from other regions (mature and embryonal tissue) which may be observed in the living state, but we shall also hereafter make use of this method in the decision of other controversies about the cornea. Let us now return to the closer consideration in the fresh state of the cells which unite to form the cellular network of the cornea. It has been stated that when perfectly fresh these cells in all their parts possess a refractive power so equable with that of the corneal substance, that in this state it is quite impossible to see them.

It is, however, important to know that when the cornea commences to lose its complete homogeneity, as gradually takes place in the examination in the moist chamber with humor aqueus as the medium, still the corneal corpuscles do not immediately forfeit their vital characteristics. On the contrary, it is much easier to convince ourselves of their contractility at a time when they are distinctly visible. I have indeed never seen spontaneous changes in form under the circumstances in which Kühne * saw them; changes which, according to his statements, take place very slowly, so that we can only be assured of them by the use of the camera lucida. I must, however, affirm that a contraction of the corneal corpuscles may be caused by induction shocks; thus I should be an upholder of Kühne's teaching against Engelmann and others, if it were not that I differed so essentially from him in the description of the appearances. Further experiments † led me to employ a few powerful opening induction shocks as the best method of irritation. These are obtained from an induction apparatus (primary coil of 160 turns, a core of iron wire, and a secondary coil of 6,245 turns), which is set into activity by two large chromic acid and carbon elements coupled with the homonymous poles. The secondary coil is to be thrust quite home upon the primary coil. A series of such shocks cause a diminution of the cell-body as seen from the surface, and partial withdrawal, but generally only a drooping, of the processes of the cells. These appearances in the protoplasma of the cell are not, however, the most striking result of the electrical irritation; the most striking appearance is rather this, that suddenly the outlines of the serous canaliculi (corneal tubes) described by v. Recklinghausen become visible in the cornea, so that I must regard the electrical irritation as a true experi-

* L. c., p. 125.

† Golubew, *Archiv f. mikr. Anat.*, Bd. v., pp. 55 and 56, and this text-book—pp. 58, 84, and 85.

mentum crucis for the existence of this much-talked-of structure. The visibility of the canaliculi depends, however, upon the above-mentioned contraction of the protoplasma of the corneal cells. We shall become better acquainted with the results of electrical irritation hereafter, in speaking of the canaliculi.

We must here make mention of the active movements of the corneal corpuscles which may be observed in inflamed corneæ, the cornea being constantly inundated with blood-serum (Stricker and Norris); * also of the retraction of the processes of the corneal corpuscles upon the application of a four per cent. solution of phosphate of soda (v. Recklinghausen),† which appearance cannot well be considered as due to shrinking, since the corpuscles retain their stellate form when treated with more concentrated solutions.

In the preceding there are sufficient positive statements concerning the corneal corpuscles, with which the opinions advanced by Schweigger-Seidel are inconsistent. We shall hereafter refer to two experiments by Schweigger-Seidel, which were intended to isolate the cell-plates described by him; these experiments are the injection of the cornea by the method of simple penetration with iodine-serum, a watery solution of sugar or diluted alcohol, and also the boiling of the cornea in alcohol containing a little hydrochloric acid. Also the lines of Hoyer in the serous canaliculi, upon which Schweigger-Seidel relies, will hereafter be spoken of. In view of the numerous means which we possess for rendering visible the protoplasmic network of the cornea, and also in view of the typical repetition of the appearances of this protoplasmic network in every cornea examined, it will seem singularly bold, to one who employs the deductions of analogy as an aid to reason wherever those deductions are in reality admissible, that Schweigger-Seidel, in the face of every manifest analogy, should attempt to explain the stellate corneal corpuscles as pseudo-cells depending upon the proliferation of a peculiarly distributed interfibrillar cement.

The behavior of the corneal corpuscles in inflammation, and the origin of the wandering cells.—The behavior of the corneal corpuscles in inflammation is of radical importance in the decision of the controversy just mentioned. Before we gave up the consideration of the wandering cells, we glanced over the various theories which have been advanced from time to time. We were thus led at last to the researches of Stricker and Norris.‡ These authors have shown that corneæ cauterized and treated at various times after the cauterization with chloride of gold, which colors the wandering cells as well as the corneal corpuscles, present appearances which demonstrate a considerable multiplication of nuclei in the corneal corpuscles. The corneal corpuscles are transformed into masses containing many nuclei, and other pictures make it highly probable, from the relations of the corneal corpuscles and the wandering cells at the same point, that the latter are developed from the former through the intermediate stage of the masses with many nuclei.

Corneæ cauterized and examined in the iodine-chamber present the best view of the appearances described by Stricker and Norris. In fact the transition stage may be more easily and more perfectly followed by the iodine-absorption. Besides the experiments on corneæ that have been cauterized with nitrate of silver, or inflamed by the passage of threads, it is also advisable to conduct experiments in such a way that the iodine itself may excite inflammatory action.

Take for example the entire freshly amputated cranium of the Frog, the

* L. c., p. 4. † Virchow's *Archiv*, Bd. 28, p. 179. ‡ L. c.

nictitating membranes having been previously removed, and place it with proper support in a large iodine chamber; let it remain there till the corneæ become perfectly brown, which requires several hours. Then examine the excised cornea in humor aqueus, after removal of the anterior epithelium. The picture is a very remarkable one. The nuclei of the corneal corpuscles have lost their usual shape, they appear in the most remarkable elongated, indentated, branched forms, and very smooth and brilliant. Some of the nuclei seem to be deeply notched, others have in reality been resolved into several roundish nuclei. The first-mentioned picture accords evidently with those appearances of the nuclei which F. A. Hoffmann* remarked in inflamed corneæ, and of which he states that they exactly resemble wandering cells, and that he considered them as contractile portions of protoplasm from the stellate cells.

If we bind the living Frog, from whom the nictitating membranes have been removed, in such a way that the head is in a vessel containing moistened iodine, and thus expose the corneæ to the influence of the iodine vapor, it usually requires a long time before an intense iodine color appears in the eye; but the corneæ may be excised, and colored still more in the iodine chamber. The transition stages between corneal corpuscles and wandering cells may be excellently followed in the corneæ of Frogs thus treated.

As has been already stated, the appearances described by Norris and Stricker were in general confirmed in a large number of corneæ cauterized with nitrate of silver and examined in the iodine chamber. But it also appears, as Stricker† has remarked, that very varying inflammatory phenomena present themselves in corneæ, which in all important respects have been subjected to precisely the same treatment: and, what is of great importance, it is certain that in a few cases a copious purulent infiltration begins at the margin of the cornea, at a time when as yet but little, if any proliferation of the corneal corpuscles can be recognized at the point of cauterization, and this infiltration on the other hand is entirely wanting in other cases. In the former class of cases the appearances are such as may have presented themselves to Cohnheim, with reference to the relations between the corneal corpuscles and the pus corpuscles.

However certain therefore it is that the formation of pus may commence with the corneal corpuscles, and however decisive this fact may be for the protoplasmic nature of the latter, it is also equally certain that a purulent infiltration of the cornea may be developed without any participation of the corneal corpuscles.

We must accept two different sources for the wandering cells of the cornea, and if we have not followed a particular inflammatory process from the beginning up to a certain moment, then it will not be possible in a given case to say how many are derived from the one source and how many from the other, or how many have their origin in the division of the wandering cells already existing (Stricker).‡

As regards the wandering cells present in the normal uninflamed cornea, it has not been proved that they have their origin in the corneal corpuscles. The cells which form the eruptive nodules lying immediately between the anterior epithelium and the corneal tissue in Keratitis phlyctænularis, and reach along the nerves at that place (Iwanoff),§ appear to be only wanderers from the blood.

The fibrillar substance (*fibrillar portion of the basis substance*) *of the cor-*

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* L. c., p. 212. † *Studien*, p. 34. ‡ L. c., p. 18.
§ *Klinisches Monatsblatt für Augenheilkunde*, vii. Jahrgang, p. 462.

neal tissue.—The fibrillar substance represents the preponderant element, in point of volume, of the corneal tissue.

At a time when the cells in the cornea had been but little observed, although a very effective use had already been made of the microscope in the examination of animal tissues, the substance of the cornea propria was considered simply as a tissue composed of fibrous bundles (Valentin,* Donné,† Henle,‡ Pappenheim,§ Brücke,‖ and others). In former times a laminated structure was generally ascribed to the cornea; thus Haller described it as consisting of many laminæ.

These laminæ corneæ of the old anatomists seemed to come into the foreground again with fresh confirmation, when Todd and Bowman¶ designated the cornea propria as "lamellated cornea" and distinguished a series of sixty lamellæ in the Human cornea.

Todd and Bowman, however, designated their corneal lamellæ as "a peculiar modification of the white fibrous tissue" (fibrillar connective tissue) of the sclerotic, with which the lamellæ were said to be directly continuous. The individual lamellæ are also said to be so intimately bound together by numerous filaments of a similar nature that it is impossible to follow the course of a particular lamella, or at least only for a short distance. When we review this description, the question instantly arises whether, with the condition of affairs portrayed by Bowman, the designation "lamellated cornea" may not be improperly chosen. Bowman** afterwards describes the fibrous tissue in a similar manner. Although we find Bowman quoted for the microscopical proof of a lamellated structure of the cornea, and hear of the lamellæ of Bowman, still a lamellated structure of the cornea, to which this designation could be applied in a clear and consistent manner, was first vindicated in 1852 by Henle†† in opposition to views previously held by him.

According to his description the substance of the cornea was formed by "homogeneous lamellæ," whose number, however (about 300), far exceeded the estimate of Todd and Bowman, and all of which ran parallel to the surface of the cornea. A further explication of the views held by Henle at that time is given by Dornblüth.‡‡

Shortly before the appearance of Henle's later views, another opinion concerning the structure of the corneal tissue sought to gain a foothold; for, following the teaching of Virchow concerning the connective tissues, Reichert's views on the structureless character of the fibrous connective tissue in contradistinction to the connective-tissue corpuscles, and on the basis substance (fibrillar substance), considered simply as intercellular substance, seemed to receive material support in a genetic point of view. The basis substance of the corneal tissue was also said to be a structureless mass divided into bands and striæ by the rows of cells (Strube).§§ But His‖‖ approached again the former teaching when he described the corneal lamellæ as capable of subdivision. Kölliker,¶¶ in opposition to the two last-mentioned views, maintained the theory of the fibrous nature of the cornea. Classen*** and Rollett††† likewise defended the fibrous structure of the substantia propria corneæ, and more recently Engelmann‡‡‡ and Schweigger-Seidel§§§ have done the same. Meanwhile Langhanns‖‖‖ under Henle's direction, and Henle¶¶¶ himself have confirmed the idea that the lamellæ, formerly considered homogeneous, are composed of the finest fibres. But Henle, besides giving due importance to the laminated arrangement of the fibrillar substance of the cornea, also makes the artificial and undemonstrable distinction of primary and secondary corneal lamellæ.****

At the present time the corneal tissue is generally described as possessed of a fibrous structure.

In point of fact, if we tear up under water a piece taken from the centre

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* *Repertorium der Physiologie*, 1836, p. 311. † *A. Institut*, 1837, Nr. 220.

‡ *Allgemeine Anatomie*, Leipzig, 1841, p. 320.

§ *Specielle Gewebelehre des Auges*, Breslau, 1842, p. 55. ‖ L. c., p. 9.

¶ *The Physiological Anatomy and Physiology of Man.* London, 1845 and 1847, p. 17.

** *Lectures*, etc., p. 10.

†† Canstatt's *Jahresbericht für*, 1852. Bd. i., pp. 26 and 27.

‡‡ Henle and Pfeiffer, *Zeitschrift für rationelle Medicin*, N. F. Bd. vii. and viii., pp. 156 and 212. §§ L. c. ‖‖ *Beiträge*, etc., p. 12.

¶¶ *Mikroscop. Anatomie*, ii. Bd. 2. Hälfte, pp. 608—610, and 613—615.

*** *Ueber der Histologie der Hornhaut*, Rostock, 1858, p. 25.

††† *Sitzungsbericht der Wiener Academie*, Bd. xxiii., 1859, p. 516.

‡‡‡ L. c., p. 1 and 5–6. §§§ L. c., p. 307. ‖‖‖ L. c., p. 9.

¶¶¶ *Eingeweidelehre*, p. 595. **** L. c., p. 592 and 593.

of the fresh cornea, we shall always meet with striated bands or trabeculæ, and also smaller fibrous bundles or single fibres which we recognize as component parts of the former. The fact that the bundles and fibres thus brought to view by mechanical means presented the appearance of being elementary formations, led to the theory of the fibrous structure of the cornea. The bundles and fibres of the corneal tissue, like those of the fibrillar connective tissue, may be isolated, not only by mechanical means but also by certain chemical reagents; and in the latter case, as well as the former, the objections raised against the pre-existence of the fibrillæ have been most effectually met.

The resolution of the corneal tissue into fibrillæ succeeds best with a solution of permanganate of potash, or a mixture of this with alum (Rollett),* a reagent which also resolves very beautifully the fibrillar connective tissue. Portions of cornea treated with this solution acquire a brown color, and when agitated in water resolve themselves into longitudinally striped, band-like bundles (fig. 349), and these subdivide into smaller divisions and single fibrils corresponding to the longitudinal striæ.

Fig. 349.

Fig. 349. Isolated fragments of corneal tissue from the cornea (of the Ox), treated with permanganate of potash—slightly magnified.

The analytic action of the permanganate of potash depends upon the fact that the substance of the corneal fibrils is more resistant than the other substances of the cornea, namely, the interfibrillar portion of the basis substance and the cells.

Portions of corneal tissue treated with permanganate of potash do not give the so-called xanthoproteinic acid reaction (Rollett),† though this is the case with portions of fresh corneal tissue; these acquire throughout a yellow color when boiled with nitric acid with the addition of ammonia.

Also maceration of sections of fresh cornea in a 10 per cent. solution of common salt renders the fibrils easily isolable (Schweigger-Seidel);‡ at the same time myosine passes into the salt solution, and may be extracted therefrom by the addition of powdered salt or the addition of water.

Bruns § first extracted myosine from the cornea, and attributed it to the corneal corpuscles. He believed that thus he had furnished a chemical support to the views entertained by Kühne concerning the contractility of the corneal corpuscles. Schweigger-Seidel,‖ doubtless under the influence of the teaching concerning the corneal cells maintained by himself, denies that the myosine is derived from the cells. Kühne¶ states that watery extracts of the cornea contain a great deal of paraglobulin, which probably comes from the corpuscles. A. Schmidt,** by the addition of fragments of the fresh cornea, caused coagulation in transudations. Funke †† believes that he has demonstrated albuminate of soda, albumen, and casein in the watery extract of the cornea. Bruns ‡‡ also obtained alkaline albuminate from watery extract of the cornea, and attributes it to the fluid which permeates the

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* L. c., p. 519. † L. c., p. 523 and 524. ‡ L. c., pp. 308 and 352.

§ *Medicinisch chemische Untersuchungen.* Herausg. von F. Hoppe-Seyler. 2 Heft. Berlin, 1867, p. 260. ‖ L. c., p. 352.

¶ *Lehrbuch der physiologischen Chemie*, p. 386.

** *Archiv* von Reichert und Du Bois. 1861, p. 675.

†† *Lehrbuch der Physiologie.* 2 Aufl. 1858. Bd. ii., p. 160. ‡‡ L. c.

corneal substance. As appears from the foregoing, our knowledge concerning the distribution of the albuminous substances in the cornea leaves much to be desired. Moreover it is not proven that, with the albuminous substance contained in the watery extract, everything is extracted from the cornea which is destroyed when the so-called xanthoproteinic reaction disappears under the influence of permanganate of potassa.

The fibrils of the corneal tissue are very fine (at the most 0.0001 mm. in thickness, Engelmann),* and arranged in broad but thin band-like bundles which in most parts of the cornea run parallel with the surface of the cornea, or nearly so. In these portions of the cornea such bands lie in thin layers one above the other. The direction of the fibrils in these bands varies; they cross one another at different angles, often at right angles (fig. 350); the superimposed bands are joined together, often very closely, by fibrils which pass from one band to another.

Fig. 350.

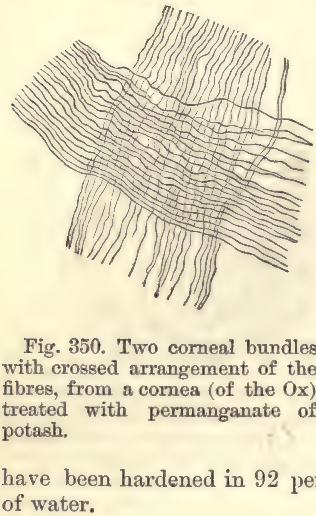

Fig. 350. Two corneal bundles with crossed arrangement of the fibres, from a cornea (of the Ox) treated with permanganate of potash.

In the vicinity of the external surface of the corneal tissue, in some animals commencing sooner than in Man, the fibrous bundles of the cornea take a course inclined toward the surface. At the same time they interweave themselves very closely, so that sections perpendicular to the cornea intersect them in the most various directions (fig. 351).

In such sections bundles cut longitudinally, as they arose from the deeper layers to the surface of the cornea, have been improperly considered as something different from the fibrillar substance of the cornea. The so-called supporting fibres or fibræ arcuatæ are nothing but bundles of fibrils which have taken the above-mentioned irregular course. They are very well to be seen in sections of corneæ which have been hardened in 92 per cent. alcohol diluted with an equal quantity of water.

Fig. 351.

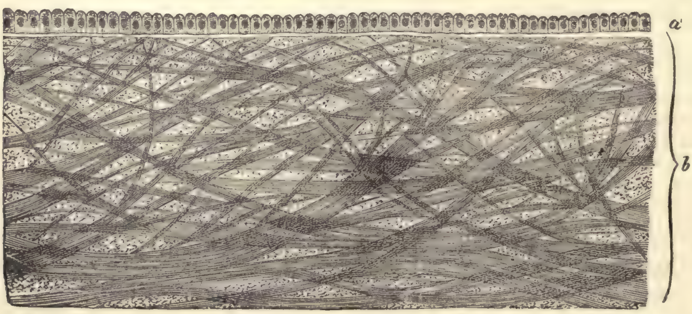

Fig. 351. Section from a cornea (of the Ox) hardened in dilute alcohol, and examined in water; *a*, innermost layer of the anterior epithelium; *b*, external layers of corneal tissue with the fibræ arcuatæ (supporting fibres).

* L. c., p. 1.

Such sections, made on a cork with one stroke of a sharp knife, and examined in water, show also that the substance between the fibræ arcuatæ exhibits fine punctate markings.

These markings correspond to fibres cut transversely. In like manner may be seen, in corneal sections thus prepared, bands of the deeper layers running parallel to the surface of the cornea, sometimes longitudinally cut and sometimes transversely; in the latter case they show a fine punctate marking instead of a striation corresponding to the fibrillæ. These transversely cut bands, however, seem to be limited. They present long, thin stripes, lying between the longitudinally striated layers above and below, which converge at the pointed ends of the transversely cut bands. Consult also Henle * and Schweigger-Seidel † on the appearances presented by the transversely cut bands of the cornea.

Between crossed Nicol's prisms the transversely cut bands appear dark in every azimuth, while the longitudinally and obliquely cut bands appear alternately light and dark (His).‡ The optical axis therefore corresponds with the direction of the fibres; compare Boeck § and Müller.‖ The entire cornea, as free from folds as possible, and with its natural curvature, when examined between crossed Nicol's prisms presents a dark cross (Brewster,¶ Valentin), ** which does not change its position when the cornea is revolved on an axis standing at its summit and perpendicular to its surface (optic axis).

This indicates a preponderance of fibres or fibrous bundles running in a meridional direction over those which run in all other directions. On this supposition the explanation of the cross is as follows: In each of the doubly refractive meridians one plane of polarization passes through the axis of the cornea (optic axis), the other lies perpendicular to the former. Between crossed Nicol's prisms all those meridians must appear dark whose plane of polarization coincides with those of the analyzer and polarizer, but the intervening meridians will be the lighter the more distant they are from the dark meridians. ††

Let us now take into more careful consideration that layer of the corneal tissue which is situated immediately beneath the external epithelium. In sections through the Human cornea it presents the appearance represented in fig. 345, between *b*, *b′*.

Reference has already been made to the similarity in appearance of this layer with the membrane of Descemet. It has also been considered as the analogue of the membrane of Descemet, and as such it was called by Bowman ‡‡ lamina elastica anterior, and by Henle §§ external basal membrane.

The existence of this layer cannot be denied, and Langhanns ‖‖ was in error when he mentioned me among those who had denied it.

I have, however, denied,¶¶ and still deny that this layer presents the same conditions with the membrane of Descemet. It does not therefore merit the above-men-

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* *Eingeweidelehre*, p. 595, fig. 454.

† L. c., p. 309, figs. 1 and 3.

‡ L. c., p. 28.

§ Taf. ii., fig. 1.

‖ *Zeitschr. für rat. Med.* 3te Reihe. X. Band, p. 173.

¶ *Philos. Transactions.* 1816, p. 315.

** *Untersuchung der Pflanzen- und Thiergewebe im polarisirten Lichte.* Leipzig. 1861, p. 270.

†† Compare v. Lang, "On the cross shown by certain organic bodies in polarized light," etc. Poggendorff's *Annalen*, Bd. cxxiii.

‡‡ L. c.

§§ L. c., p. 605.

‖‖ L. c., p. 19.

¶¶ L. c., pp. 524 and 525.

tioned names. It might be called, according to J. Arnold,* the sub-epithelial layer of the cornea, or the anterior limiting layer of the corneal tissue (Reichert).

In the Human cornea, and that of various animals, treated with permanganate of potash, this layer is resolved into the same fibrils as all the other substance of the corneal tissue, while at the same time the membrane of Descemet under the same influences retains its elastic quality of rolling inwards, hereafter to be described, its splintery cleavage, and its structureless appearance.

The anterior limiting layer † is simply a peculiarly dense layer of corneal tissue, composed of many closely interwoven fibrils which cross each other at various angles. This layer is not everywhere equally broad. It is highly developed in Man, less so in the Sheep, the Ox, and the Pig, better developed again in the Dog and the Cat.

It is evident from the description already given of the structure of the basis-substance of the cornea, that there can be no question concerning corneal lamellæ, properly so called. In that case it would be necessary to designate the smooth bundles themselves as lamellæ, which has in fact been done, but improperly.

The appearance of a lamellated structure, and the ready cleavage of the cornea in the direction of its surface (especially in corneæ hardened in dilute alcohol or Müller's fluid) depends upon the flat arrangement and stratification of the smooth fibrous bundles of the cornea; but these are united in many places by filaments passing in a direction perpendicular to the surface. We shall hereafter speak of those portions of the superimposed bundles which are not thus united, and which promote the above-mentioned cleavage.

The fibrils of the cornea, and the bundles formed by them, distend when macerated in water, at the same time increasing in thickness. In acids also (acetic acid, pyroligneous acid, very dilute hydrochloric acid) they increase in thickness, the fibrils and bundles are crowded closely together, and lose their striæ, while the cells, assuming a granular appearance like the cells of connective tissue when treated with acids, become plainly visible in their continuity.

Dilute alkalies likewise cause the corneal fibrils to swell up.

When boiled in water the cornea shrinks considerably in a radial direction, but compensates by increasing very much in thickness. Here the fibril bundles behave exactly like those of the connective tissue, and here also, if we dry the partially cooked cornea and prepare sections of it, which are afterwards to be moistened again, the cells will be very distinctly seen. In former times this method was extensively employed for the demonstration of the corneal corpuscles.

Whether the cornea is distended by the action of acids or by boiling, those bundles which take a course inclining toward the surface, owing to the fact that the mass of bundles running parallel to the surface are so greatly thickened, are stretched and strained in the direction of the longitu-

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* *Die Bindehaut der Hornhaut und der Greisenbogen*, Heidelberg, 1860.

† In this relation it represents the analogue of that which in the skin is described as corpus papillare, by Henle as intermediary skin, by Krause as superficial layer of the corium, by Bowman as basement membrane or tunica propria cutis, by Kölliker and Gerlach as superior layer of the corium, by Virchow as superficial layer of the corium of the nail matrix, by Leydig as homogeneous limiting layer of the epidermis. Compare my remarks in "Researches concerning the structure of connective tissue." *Sitzungsber. der Wiener Akademie*, Bd. xxx., p. 50.

dinal axis so as to be mechanically hindered * from undergoing the same changes as the other fibrous bundles of the cornea. Upon this cause, and not upon any essential difference between the fibræ arcuatæ and the other bundles of corneal tissue, depends the peculiar appearance presented by the fibræ arcuatæ in the corneæ which have been either boiled or macerated in acids.

If we boil the cornea continuously, restoring from time to time the evaporated water, or heat it for some time in an oil bath at a temperature of 100° C., sealed in a glass tube with a little distilled water, a considerable portion of the corneal substance is dissolved.

Meanwhile the membrane of Descemet remains for a long time completely unchanged, although after four or five hours of boiling the fibrillar substance may have entirely disappeared without leaving a trace even of the lamina elastica anterior.† The solution, when separated by filtration from the undissolved residue, solidifies like the solutions of gelatine.

The reactions of the solution are somewhat different from those of an ordinary solution of gelatine.

Joh. Müller ‡ states that the substance contained in the solution is identical with the chondrin from hyaline cartilage. This opinion, however, will be hereafter disputed.

If the gelatine from the cornea were identical with the chondrin of the hyaline cartilage, then chondrin would be derived from two entirely distinct substances; for the fibrillar substance of the cornea when treated with water, alkalies, and acids, presents reactions essentially different from those of the basis-substance of the hyaline cartilage. In the latter respect it corresponds much more with the fibrils of the connective tissue, but it will be hereafter shown that it differs essentially from this also.

According to Kühne,§ the corneal gelatine is distinguished from chondrin only by the fact of its not being precipitated by acetate of lead, and by its turbidity when treated with tannic acid. His ‖ thought that the corneal gelatine might be distinguished from chondrin by its ready resolution when treated with an excess of the reagent that had precipitated it. But Bruns¶ obtained different results. Although by heating with hydrochloric acid he could not extract any cartilage-sugar (chondroglycose) from the corneal gelatine, he found the specific reaction to be almost identical with that of chondrin. Finally, Schweigger-Seidel ** obtained from corneal gelatine, extracted with a 10 per cent. solution of common salt, at one time no chondrin reaction; at another time, after brief action of the salt solution he found it. Concerning the chemical nature of the fibrillar substance of the cornea and the structures derived from it we have therefore, as yet, no settled views.

On the relation of the cells of the corneal tissue to the basis-substance; the interfibrillar portion of the basis-substance and its interstices.

Natural cavities in the basis-substance of the cornea occur only in the form of the serous canaliculi (corneal cavities), demonstrated by von Recklinghausen; †† and these enclose the corneal cells.

Exact researches concerning the serous canaliculi were first made on corneæ which had been treated with solutions of the nitrate of silver.

The obvious result of the silver treatment of the cornea, without regard to the chemical nature of the process, appears to me to have but one meaning,‡‡ that is, if the preparation has been successful. Unsuccessful silver

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* Compare A. Rollett, *Berichte der Wiener Akademie*, Bd. xxx., pp. 60–66.

† Compare Schweigger-Seidel, l. c., p. 355.

‡ Poggendorff's *Annalen*, Bd. xxxviii., p. 513.

§ *Physiolog. Chemie*, p. 386. ‖ L. c. ¶ L. c., p. 263.

** Pp. 355 and 356. †† *Die Lymphgefässe*, etc., pp. 36–52.

‡‡ By this we do not mean to pass a similar judgment on the silver markings of other objects.

preparations can here claim, as I believe, no higher worth than unsuccessful preparations in every other method of histological research.

Let us begin with the negative (Leber *) silver pictures. These may be very nicely obtained if the perfectly fresh cornea of any animal be immersed for a short time—the proper length of time should be specially tried for the different corneæ—in a dilute solution of nitrate of silver (2—8 grains to the ounce of water), and then exposed in water to the action of the light; the rapid working of the sunlight is of essential aid in getting successful and convincing preparations.

Also a prolonged maceration in water before the examination must be avoided. Prolonged soaking in water produces in silver preparations an innumerable quantity of diverse and inexplicable appearances.

If we examine the cornea immediately after it becomes thus rapidly brown, we shall see in the browned basis-substance white spots, from which white processes spread out in every direction (His,† von Recklinghausen); ‡ the processes anastomose with one another, and in general we have a picture which reminds of the protoplasmic network of the corneal corpuscles, except that the outlines of the nodules and processes which compose the plexus are more sinuous and less straight than, for instance, in the network displayed by the gold treatment. Compare fig. 352 with fig. 348, *a*.

The statement of His § that the silver figures of the cornea coincide with the form of the cells is, under some circumstances, quite correct. But this is not always the case (v. Recklinghausen), ‖ and for this reason, that the protoplasm of the cell may entirely or partially withdraw itself from the wall of the cavity. The assertion that the silver figures do not generally

Fig. 352.

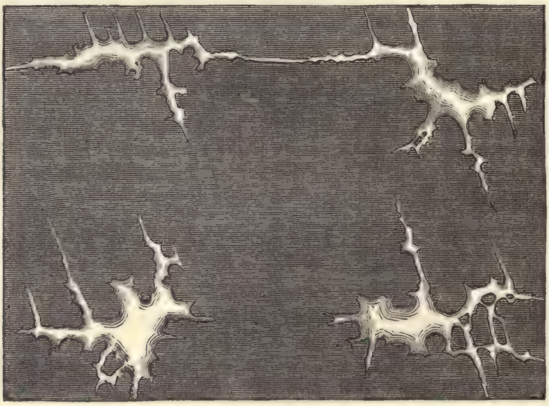

Fig. 352. From the Frog's cornea, treated with nitrate of silver.

coincide with the stellate corneal corpuscles, because the latter in humor aqueus exhibit but few ramifications of their processes, while the silver figures present a very densely woven network (v. Recklinghausen),¶ we cannot accept as true, in view of our statements concerning the protoplasmic network displayed by corneæ which have been left in the nictitating

* L. c. † Virchow's *Archiv*, Bd. xx., p. 207. ‡ L. c.
§ L. c. and *Schweizerische Zeitschr. für Heilkunde*, l. c.
‖ L. c. ¶ See this text-book, pp. 225 and 226.

fold, or in an atmosphere saturated with watery vapor, or which have been treated with the chloride of gold or iodine vapor. Von Recklinghausen * demonstrated in these silvered spots by carmine-staining red flakes, which sent out processes in one portion of the network, while another portion was empty or contained only small red, somewhat brilliant granules. These flakes, with their processes, and the red granules, were the remains of the protoplasmic network of the cornea, which in silver preparations may present very different degrees of alteration.

In order to arrive at a full understanding of the silver markings in the cornea, it is of great importance to carefully note the working of the silver from the beginning. This may be best done if we treat corneæ already silvered (with a solution containing two grains of the nitrate of silver to the ounce of water) also with the chloride of gold (two grains to the ounce).

Upon immersion into the latter solution the brown color of the basis-substance disappears immediately. If the cornea, after remaining in the solution the usual time for the gold treatment, be exposed to the action of the light in water weakly acidulated with acetic acid, it rapidly assumes a blue color. This reduction is caused, as may be easily seen with the microscope, by the basis-substance. The same stars with their processes appear in the blue basis-substance as in the silvered pictures. An essential fact is it, however, that both cell-substance and nucleus, when they still survive, are rendered visible by means of the impregnation with the chloride of gold by a distinct granular appearance and a faint yellow color. We may thus convince ourselves that where the nitrate of silver has worked for only a short time, the corneal corpuscles are still plainly visible, though in a somewhat swollen state, filling up the clear interspaces in the basis-substance and their processes. If the action of the silver has lasted longer, or if the cornea has been soaked too long in water, which should be avoided, the cells and their processes appear even more swollen, and at the same time the interspaces of the basis-substance are correspondingly altered. If the cornea has been subjected to the action of the nitrate of silver for a still longer period, the intervals in the basis-substance, even when subsequently treated with the chloride of gold, appear empty; the cells are destroyed. We shall hereafter refer again to these same preparations. For this purpose we recommend also the staining of the already silvered cornea with hæmatoxylin, but do not consider it preferable to the combined silver and gold treatment.

I have previously stated that when the cornea is subjected to irritation by electricity, the most striking phenomenon is the distinctness presented by the outlines of the cavities in the basis-substance.† Owing to the clearness with which I observe this phenomenon, and to the fact that it may always be demonstrated without failure, it is difficult for me to understand why it has not been heretofore noticed.

If we bridge a freshly excised cornea over platina electrodes, in humor aqueus from the same eye, and cover it with a glass cover, the edges of which have been greased, and then slowly apply a few opening shocks as described above, we shall soon see the previously homogeneous cornea, or marked only by the faint outlines of a few stellate cells, assume the appearances represented in fig. 353.

Bright figures, straight or curving, elliptical, spindle-shaped, or round,

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* *Die Lymphgefässe*, p. 38.

† A. Rollett. "On the contractility of the corneal corpuscles and the corneal tubes." *Centralbl. für die med. Wissensch.* 1871. No. 13.

make their appearance. The round and elliptical figures are to be distinguished as sharp perforating holes. These bright figures are simply longitudinal, oblique, or transverse sections of the system of communicating channels, which traverse the cornea, and at whose enlarged nodal points may be found the nucleated centres of the stellate corneal cells. This may be very distinctly seen if we attempt to adjust the focus exactly for one of the corneal corpuscles; we shall then see, as in fig. 353, the finely granular protoplasm of the cell-body retracted from the walls of the more extensive cavity in which it lies, in general taking the form of the cavity, and permitting also some of its processes to be followed into those of the cavity. All things considered, we here have a picture of the relations between the protoplasm and the cavities of the basis-substance, exactly like that often presented in embryonal bone between bone-cavities and their cells.

Fig. 353.

Fig. 353. From the Frog's cornea, which has been subjected to powerful induction shocks (highly magnified).

By a successful experiment such as that mentioned above, and with me, as I have said, the experiment succeeds almost every time, any one may convince himself of the correctness of my statements. The preparation must be examined with an immersion lens of high power. The irritated cornea should be quickly exposed to iodine-vapor or to the gold treatment, and the picture thus obtained should be compared with that of the unirritated cornea, and it will be impossible longer to have doubts concerning the state of affairs in the cornea. The corneal cavities which thus come to view cannot be explained by the arrangement of the fibrillar substance alone.

Either there exists in the corneal tissue a canal system limited by a special membrane, from the inner surface of which the protoplasm has the power of retracting itself, and this membrane is in and of itself capable of retaining its own form, or is firmly attached by its external surface to the fibrillar substance, or, on the other hand, the corneal cavities are embedded in a substance which exists between the fibrils and fibril-bundles; this substance is traversed by a network of tubes with dilated nodal points, and this system of tubes is sometimes completely and sometimes incompletely filled by the protoplasmic network of the corneal corpuscles.

Such a membrane as is called for by the first supposition, a special cell-membrane or encysting membrane of the cellular network of the cornea, can neither be demonstrated in fresh preparations by a double contour in transverse sections, nor by tearing off and spreading out fragments of the lacerated membrane. In regard to the second supposition, it explains perfectly the appearances presented by the fresh irritated cornea.

The signification of the appearances obtained by the silver treatment and other methods of impregnation—always with reference to the morphological appearances—presents in general no difficulties if we always bear in mind the three factors, namely, the protoplasmic network, the corneal cavities, and the substance in which the cavities seem to be embedded and which is traversed by the fibrils. We cannot here enter more fully into the chemical process, namely, of the action of the silver; none of the hypotheses on this point are satisfactory.

The recent statement of Genersich,* that wandering cells might gain access to and move about in the corneal cavities which are revealed by the silver treatment, coincides with results obtained by us; so also the researches of Hansen,† who found corresponding changes in the corneal cavities accompanying the inflammatory changes in the corneal corpuscles.

Whether at the margins of the corneal cavities there exists anything similar to the arrangement in the bone cavities ‡ and dentinal canals (dentinal sheaths), § as some observations seem to indicate, I am not able to decide from the attempts at isolation already made by myself, but I do not consider it as probable.

Experiments with injections, and inferences drawn from the results obtained by them, play an important part in the consideration of the corneal structure, (Bowman,‖ v. Recklinghausen,¶ Leber,** C. F. Müller,†† Schweigger-Seidel,‡‡ Boddaert). §§

Boddaert (l. c.), as it appears, first succeeded in filling the corneal cavities with an injection by puncture. Whether an injection of them exists by capillary action, as was maintained (v. Wittich) ‖‖ for the formerly accepted intracellular spaces of the corneal network, must be decided by fresh researches adapted to the more recent views.

The ordinary result of all injections by puncture is a splitting of the corneal tissue. These experiments, owing to the peculiar structure of the cornea, and the regular, but in different directions unequally firm cohesion of its fibrous masses, result in a quite characteristic distribution of the injected substance. Hence arose the false conclusion that in the fresh cornea there existed long, straight, tubular spaces (the corneal tubes of Bowman,¶¶ interlamellar spaces of Henle), *** or a plexus-like system of canals (v. Recklinghausen,††† C. F. Müller,‡‡‡ Schweigger-Seidel). §§§

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* *Medicin. Jahrbücher der Gesellsch. der Aerzte in Wien*, 1871, p. 1.

† *Anzeiger der Gesellschaft der Aerzte in Wien*, No. 3, 1871.

‡ See this text-book, p. 101.

§ See this text-book, p. 324.

‖ Todd and Bowman. ii., p. 19. Lectures, p. 13.

¶ *Die Lymphgefässe*, etc., p. 41.

** *Monatsblätter für Augenheilkunde*, 1866.

†† Virchow's *Archiv*, Bd. xli., p. 110.

‡‡ L. c.

§§ "Zur Histologie der Cornea," *Centralblatt für die med. Wissenschaft*, 1871, No. 22. This essay reaches me as I am correcting this sheet. It simply obliges me to alter the following passage. For the rest I must adhere strictly to my own views.

‖‖ Virchow's *Archiv*, Bd. ix., p. 90 and 91.

¶¶ L. c.

*** L. c., p. 592, fig. 448.

††† L. c.

‡‡‡ L. c.

§§§ L. c.

In view of the extensive deliberations which the various authors have held concerning the injection of the corneal spaces, the statement just made may perhaps be considered too summary. But this arises from the fact that the subject which we are treating is in reality very simple; the difficulties on the other hand have been artificially introduced; firstly, by the scarcely conceivable attempt to bring the tubular or plexus-like intervals in continuity, such as appear with splitting of the corneal tissue, into some relation with the serous canaliculi (corneal cavities); secondly, by the more intelligible effort to demonstrate lymph-spaces in the cornea, just as they have been so happily demonstrated by the same method in other tissues.

Various injecting substances may be employed for splitting the cornea. The injections with mercury (Bowman) and with oily substances succeed better than watery injections (v. Recklinghausen, Leber). The solution most to be recommended is oil of turpentine mixed with equal parts of olive oil, the latter being previously colored with ethereal extract of alkanet root. We may inject with this mixture, and be assured that all other injections give essentially the same result.

Different results will be obtained with different animals. In the cornea of the Sheep, the Ox, the Rabbit, and the Frog, we get figures densely crowded together with but small interspaces, and disposed in parallel bundles; these figures assume a lanceolate form, and generally for a shorter or longer distance in their course present irregular constrictions, but seldom communicate with one another transversely. Such bundles of figures lie one over the other, crossing each other at various angles.

In the Frog, where the injection, although difficult, still succeeds excellently in a given number of cases, the constrictions of the lanceolate figures follow each other in quick succession, leaving the intervals relatively short.

In general we have the picture which is represented with a low magnifying power in fig. 354.

All the injections succeed best in the perfectly fresh cornea, and immediately after the injection the cornea may be examined in humor aqueus (with Hartnack's objective No. 4 and eye-piece No. 3, or with higher powers).

If now we compare the appearances produced in the Frog's cornea by injection with those produced by the silver or gold treatment, we shall find it difficult, if we judge impartially, to understand why the corneal tubes should not always have been considered as essentially different from the serous canaliculi.

In all the above-mentioned animals the case is the same as in the Frog.

But the appearances are different in the Dog and Guinea-pig; here the injected substance does not form the long lanceolate figures, but arranges itself in irregularly-shaped broad spots which communicate with one another by small bands. At the margins of the puncture such spots often appear completely isolated, or are united together by very fine processes, or they enter into connection with one another by broader

Fig. 354

Fig. 354. Corneal tubes from the Frog, as displayed by the injection of an oily mixture.

bands and form an irregular plexus, which is to be distinguished only by its large meshes from those parts where the injection is more complete and the meshes are smaller.

Such plexuses lie in many layers of the injected cornea, one above the other.

When the injection is incomplete and the meshes are large we may have the appearances drawn by C. F. Müller* and Schweigger-Seidel,† from the cornea of the Guinea-pig and the Dog. Only limited portions, however, display the appearances represented in the drawings just referred to. That it is possible in such plexuses to demonstrate by hæmotoxylin-staining such a regular division of the nucleus as is shown in these drawings of C. F. Müller ‡ and Schweigger-Seidel,§ I cannot affirm from my own experience. I have never been able to obtain such results, nevertheless I consider it possible that in certain cases they may succeed; still they possess no special importance as regards the corneal structure. We must positively deny that in the cornea of the same species of animal we may obtain at one time straight lanceolate figures and at another time net-like figures, according to the force used in the injection, as is stated by C. F. Müller,‖ and as Schweigger-Seidel¶ in one place implies. This is not the case: in the first mentioned animals we always find lanceolate figures, and in the Dog and Guinea-pig always networks.

It is much more important to determine what solution of continuity has been occasioned in the cornea by the injection, than to exhibit by staining the surviving nuclei of the protoplasmic network which the injection has lacerated. This may be excellently accomplished if we separate the injected substance again from the tissue.

For this purpose it is necessary to immerse the cornea, already injected with the above-mentioned substances, in absolute alcohol. This undergoes but little discoloration, and after a few hours we may prepare thin sections, both perpendicular and parallel to the surface, with a knife moistened in alcohol. These should be soaked in ether till the injecting substance is extracted, then in alcohol, and afterwards in water, and then they may be examined after treatment with some staining solution.

The fibrillar substance of the cornea will then appear separated into laminæ, the bundles being arranged in a laminated and regularly trabeculated framework, which is tightly drawn and often broken through.

Moreover, as we pass from the fully-injected portions of the cornea to those in which the injection is only partial, we shall be able to recognize all the stages from the beginning up to complete splitting and disruption of the cornea. Nothing can now be more appropriate than the comparison of the fibrillar substance of the cornea with a compressed sponge (Kölliker).** If we should imagine that the cornea, thus split up by the injection, could be again pressed together in such a manner that all the fibrils should describe again the same course by which they left their original position, then the fibrils of this compressed sponge would have resumed their original arrangement, just as they were fastened together in the cornea by the cement substance.

We think that we have now furnished the means by which any one may convince himself that the usual result of an injection of the cornea by puncture is a splitting up of the corneal tissue.

* L. c., fig. 1. † L. c., figs. 13 and 14. ‡ L. c., fig. 1.
§ L. c., fig. 14. ‖ L. c., p. 138. ¶ L. c., pp. 316 and 317.
** *Mikroskopische Anatomie*, Bd. ii., 2. Halfte, p. 610.

The fact that the framework exhibited by this splitting is differently arranged in different animals proves that the fibrils do not follow the same course in all animals.

Schweigger-Seidel* used the splitting of the corneal tissue in the demonstration of the nucleated plates described by him; we shall hereafter show what was isolated by this method.

With reference to the incorrect theory of a system of corneal canals lined with flat cells, let us now take into consideration the appearances obtained by Hoyer,† by silvering the cornea of the Kitten, in the layers adjacent to the membrane of Descemet; appearances which C. F. Müller‡ also claims to have seen in the embryo (38–41 centimetres in length) of the Ox, also in the Dog, the Pig, etc., and in all the layers; these appearances were also described by Schweigger-Seidel,§ and drawings made from the Dog's cornea.

I am well acquainted with these appearances, but have found them only in young animals: they may be demonstrated in every young Rabbit, in the layers adjacent to the membrane of Descemet. Broad, indentated, silvered spots, continuous with one another by wide bands, display in their interior black lines, by which the spaces are subdivided in such a way as to resemble epithelial or endothelial cells bounded by silver markings. The black lines correspond indeed to the boundaries of cells. But these cells are not flat cells, but corneal cells, between which no fibrillar basis-substance, or at least but very little, has been developed.

The entire embryonic cornea at one period consists of such closely packed and at first round cells, and the transformation into corneal tissue commences at the anterior surface and gradually advances toward the posterior surface of the cornea. In young animals appearances present themselves in the layers adjacent to the membrane of Descemet, which during the period of development exist in all the layers of the cornea. But here also in the embryo of the Ox, according to C. F. Müller, and in the Sheep's embryo, as I myself have observed, we may obtain the silvered pictures described by Hoyer.

I am not able to give the exact age at which in a given animal these appearances may or may not be obtained in the layers adjacent to the membrane of Descemet, owing to the limited number of observations. It is nevertheless certain that they are not to be seen in the fully-developed cornea of the adult animal.

Great care must here be taken in the examination of silver preparations which have been macerated in water for a long time, or which have undergone degeneration; in these cases deceptive appearances of various kinds may present themselves.

The appearances described by Hoyer, therefore, are explained by the history of development of the corneal tissue, and argue as little for the existence of corneal spaces lined with cell-plates as does the splitting of the cornea by injection.

Some remarks must here be made with regard to that portion of the basis-substance of the cornea which we supposed to surround the corneal cavities with their processes (interfibrillar portion of the basis-substance). There can but little be said concerning the peculiarities and conditions of this substance, nevertheless we must bear it in mind as always continuous, and definitely but irregularly distributed in the cornea. The distribution is always dependent upon the existing arrangement of the fibrils and fibril-bundles.

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* L. c., p. 321.

† Reichert and Du Bois, *Archiv*, 1865, p. 214.

‡ L. c., p. 132.

§ L. c., fig. 16.

If we should imagine this interfibrillar substance to be inflexible and the fibrils to be removed, and the protoplasmic network also removed, we should then have the skeleton of this substance remaining.

This skeleton, however, has a particular arrangement. If we cut a perpendicular section from a perfectly fresh cornea with a sharp knife on a piece of cork, and spread the section out in water, we shall see that when the section is stretched in a direction perpendicular to the surface of the cornea, numerous interstices exist which are bounded by lengthened edges: where these interstices exist (interlamellar spaces of Henle) the bundles of fibrils are in less intimate union than in the tissue which is situated between these spaces. At the places where these spaces exist, the flat bodies of the corneal corpuscles are also to be found. If, however, we compare the length of these spaces with the length of the flat centres of the corneal corpuscles, we shall find that the former are more extensive than the latter. This substance is therefore deposited in extended layers about the interspaces which contain the corneal corpuscles, being thicker between the diverging bundles of the corneal tissue and thinner in the direction of the corneal surface, while it is more scantily distributed in the fine passages between the fibrils and about the processes of the corneal corpuscles which pass in the direction of the perpendicular diameter (fig. 348, *b*). According to the peculiar arrangement and distribution of the corneal corpuscles (comp. fig. 345 and fig. 348, *b*) these extensive flat layers of intervening substance generally take a course parallel to the corneal surface, and converging become continuous with one another, at the same time being connected by bands and filaments of various form. After having first treated the cornea with silver and afterwards with gold, as described above, we may prepare some specimens by teasing. We may then often see on certain of the fibril-bundles the markings of the edges of the still preserved or lacerated corneal cavities. The fibrils themselves, where they have been completely isolated, appear smooth, and not at all or but slightly colored. The blue color adheres to a mass which seems to be traversed by the fibrils; this mass appears to be interspersed with granules, and as on the one hand it surrounds the fibrils, so on the other hand it forms the margins of the corneal cavities.

The above-mentioned skeleton of cement substance may be isolated from the corneal fibrils, although in a distorted, ragged, and dilapidated condition. This is the case when we resolve the fibrils into gelatine by prolonged boiling in water, or in alcohol containing hydrochloric acid (strong alcohol with $\frac{1}{2}$–$\frac{3}{4}$ per cent. of smoking hydrochloric acid).

If we follow the changes which the cornea (of the Ox, the Dog, and the Sheep) thus suffers, we shall remark no further changes than the already mentioned sudden alterations in form, which are occasioned by boiling in alcohol with hydrochloric acid. The pieces of cornea become more and more free from the dissolving gelatine-yielding substance, and display, as may be shown by sections prepared from time to time, the same appearance which may be seen in boiled sections of cornea, and which have been referred to as indicating the lamellar structure of the cornea, until finally it may be easily resolved into laminæ and sublaminæ. In the direction of the perpendicular diameter are to be seen brilliant striæ, sometimes converging toward one another, here and there thickened, and lying in manifold layers one above the other.*

* Our own observations on this substance have not gone beyond this point. But to this the following remarks of Lightbody, at least in part, refer ("On the Anatomy of the Cornea of Vertebrates," *Journal of Anatomy and Physiology*, vol. i., London

When Schweigger-Seidel* states that he has succeeded, by the use of alcohol and hydrochloric acid, in bringing to view simultaneously the transparent vitreous plates of his corneal cell and the superimposed brilliant, granular-appearing corpuscle (artificial product described by Schweigger-Seidel), these appearances are due to the flat centres of the corneal corpuscles surrounded by remaining cement substance. A similar explanation must be given of the plates which can be isolated by the injection of fluids into the cornea.

With reference to the channels for the wandering cells of the cornea, we must, in accordance with the views expressed, advocate the opinion that they are to be found in the system of canals, which are also filled with the soft protoplasmic network of the corneal corpuscles (v. Recklinghausen). The idea of a fluid substance uniformly distributed throughout the cornea, in which the solid elements bathe, and in which also the wandering cells might take their path, pushing aside these elements (Engelmann),† does not accord with the appearances observed: the decision whether transudations cause or could cause disruption of the corneal tissue, after the manner of the injections by puncture, and whether in such transudations formations of an amœboid nature exist, must be left to future researches.

The Vessels of the Cornea.—The central portions of the cornea of the adult Vertebrate are destitute of blood-vessels.

In Man there exists at the margin a border of only 1–1½ mm. in breadth, filled with delicate capillary loops. These arise from arteries which run in the outer layers of the anterior portion of the conjunctiva bulbi and are continuous with the subjacent veins of the same membrane (fig. 355).

Concerning the origin of the said arteries and veins with reference to the vascular tracts of the eye, consult the article entitled Blood-vessels of the Eye.

Deeper corneal vessels, and vessels coming from the sclerotic, are not to be found in Man even at the corneal margin (Leber).

In the Human eye we may often see in the cadaver the vascular loops of the corneal margin very prettily injected. As a rule, excellent natural injections of the extended and widely-meshed loops may be seen in the fresh eye of the Sheep.

In embryonal eyes a delicate capillary plexus is to be seen on the entire anterior surface of the cornea, in that layer of the corneal tissue which lies immediately under the anterior epithelium.

Concerning lymphatics in the cornea, certain statements have been made by Kölliker,‡ His,§ and Sämisch,‖ which are founded upon isolated and

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and Cambridge, 1867, p. 16), although unfortunately he does not give his methods of preparation; he says: "The bundles are connected to each other by a gelatinous form of connective tissue which varies greatly in quantity and consistence in different animals: in the Rabbit it is abundant, but hard; in the Rat it is also abundant, but so soft, especially near the margin of the cornea, that if the conjunctival epithelium be scraped off rather roughly, it is squeezed out of place, and presents much the same aspect as Bowman's corneal tubes, which I believe are generally considered to be the artificial separation of the bundles. This gelatinous substance is dyed by carmine, though not so deeply as the corpuscles and their processes which lie embedded in it, yet deeper than the tissue composing the bundles: this last is hardly dyed at all, unless the solution of carmine is very strong, and what it does absorb then is tolerably easy to wash out."

* L. c., p. 323. † L. c., p. 6.

‡ *Mikroskopische Anatomie*, Bd. ii., p. 621.

§ *Beiträge zur normal. und patholog. Histologie der Cornea*, p. 71.

‖ *Beiträge zur normal. und patholog. Anatomie des Auges*, 1862, p. 12.

doubtful observations of the corneal margin. C. F. Müller * and Schwalbe † were not able to confirm the statements of Lightbody ‡ concerning perivas-

Fig. 355.

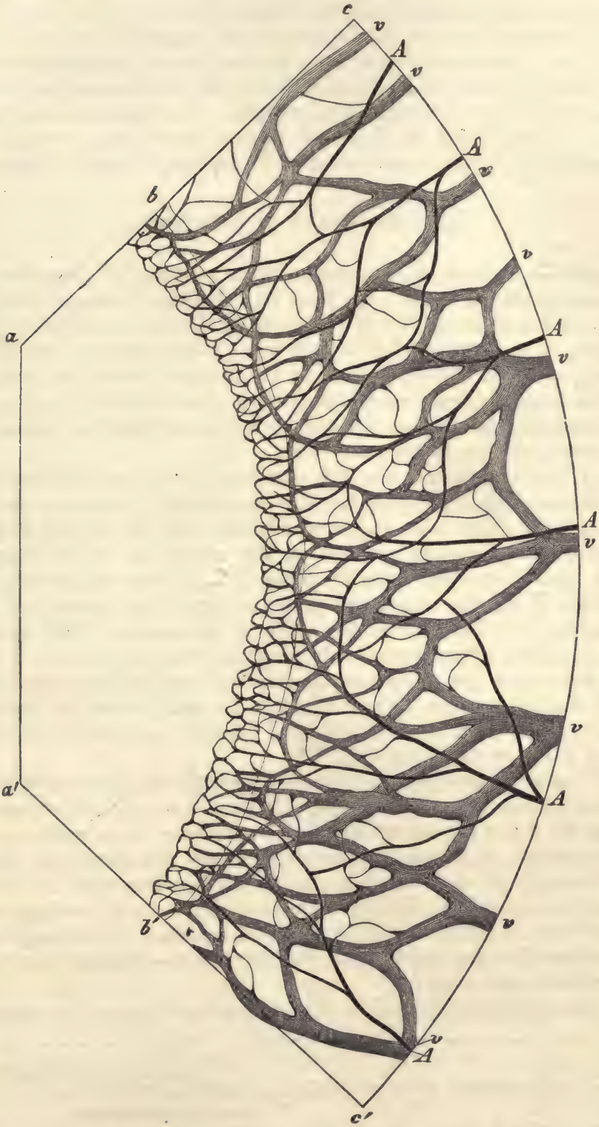

Fig. 355. Terminal loops from the most anterior conjunctival vessels, $b\ b'$. A, arteries; v, veins; $a\ a'$, $b\ b'$, cornea; $b\ b'$, $c\ c'$, conjunctiva and sclerotica. From the eye of a Child, very completely injected with gelatine and soluble Berlin blue.

* L. c., p. 147. † *Archiv für Mikroskopische Anatomie*, Bd. 6, p. 264.
‡ *Journal of Anatomy and Physiology*, 1867, p. 35.

cular spaces about the capillary loops of the margin of the cornea. The attempts to find an outlet for the fluids injected into the cornea have, as a rule, proved unsuccessful (C. F. Müller,* Schweigger-Seidel).† It is said, however, that a passage of the injected substance into the lymphatics of the conjunctiva has been observed (Leber)‡.

Finally, we must here mention the fact that when the cornea is injected by puncture, the injected substance may also be forced along the nerve trunks (C. F. Müller); § this may happen from the extravasations of injection which has been forced into the blood-vessels. In this same way may be explained (C. F. Müller) ‖ the injected figures resembling vessels, described by Teichmann,¶ also the vasa serosa of J. Arnold,** and of Niemetschek.††

The Membrane of Descemet.

In transverse sections of the cornea the membrane of Descemet presents a very sharply-defined layer. In Man its thickness increases with age. In the new-born infant H. Müller ‡‡ found its thickness to be 0.005–0.007 mm.; in the adult, at the centre 0.006–0.008 mm., at the margin 0.01–0.012 mm.; in the aged, at the centre 0.01 mm., at the margin 0.015–0.02 mm. It can be detached from the fresh cornea only with great difficulty, but quite easily from a cornea which has been treated with permanganate of potash or with a 10 per cent. solution of common salt.

Pieces of this membrane, whether obtained from the fresh cornea or from the cornea treated as above, display this peculiarity, that they curl up from the two opposite edges like paper which has lain for a long time in rolls. The margins of a detached portion of the membrane of Descemet appear under the microscope very sharply defined, and since we always get a perspective view of all the edges, owing to the great homogeneity of the membrane, it gives the impression of a vitreous substance. The membrane of Descemet has these characteristics in common with the capsule of the lens.

In the fresh state the membrana Descemetii displays no structure recognizable by the microscope. Only occasionally can be seen on the surface of fragments an indistinct and interrupted striation, parallel to the surface (Brücke,§§ Mensonides,‖‖ Leydig).¶¶

Henle*** saw the membrane of Descemet of the Ox after thirty hours' boiling resolved into a mass of the finest, rolled-up, transparent laminæ. In fine sections of the dried cornea treated for twenty-four hours with an iodine solution of the iodide of potash, Tamamscheff††† saw this membrane striated and capable of being split into the finest fibrils in the direction of the surface. Peculiar appearances have been described and drawn by Schweigger-Seidel,‡‡‡ who states that maceration in a 10 per cent. solution of common salt occasions a distinct fibrillar striation of the membrane—whether on the edge or on the surface is not stated.

At the margin of the cornea in Man there exist wart-like elevations of

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* L. c., p. 146. † L. c., pp. 324 and 325.
‡ *Klinische Monatsblätter für Augenheilkunde*, 1866, p. 17.
§ L. c., p. 142. ‖ L. c. ¶ *Das Saugadersystem.* ** L. c.
†† Prager *Vierteljahrschrift*, Bd. 3, 1864, p. 48.
‡‡ *Archiv für Ophth*, Bd. ii., Abth. 2, p. 48. §§ L. c., p. 606.
‖‖ *Nederlandisch Lancet*, Mai, 1849, p. 694.
¶¶ *Zeitschrift für wissensch. Zoologie*, Bd. v., p. 41.
*** Cannst. *Jahresber.*, 1853, p. 26, and l. c., p. 606.
††† *Centralblatt für die med. Wissenschaften*, 1869, p. 353.
‡‡‡ L. c., pp. 311 and 312, figs. 7, 8, 9, 10.

the posterior surface of Descemet's membrane (Hassal,* H. Müller).† These are wanting in the earlier years of life; between the twentieth and thirtieth year they have a diameter of 0.01 mm. at the base, are about half as high, and stand in 2–4 rows, at intervals about equal to their diameter. In aged persons they are 0.02 mm. broad at the base, 0.01 mm. in height, and form a broader zone; in rare cases they reach as far as the centre of the cornea (H. Müller).

The connections formed by the membrane of Descemet at its margins will be hereafter described.

The Endothelium of the Membrane of Descemet.

The endothelium of the membrane of Descemet (internal epithelium of the cornea) in the developed eye of Man and animals consists of a layer of polygonal cells 0.025 mm. in diameter (Henle).‡ The cells appear flattened, and possess round nuclei 0.008 mm. in diameter (Henle).§ In perfectly fresh eyes the endothelium may be brushed off in the form of a continuous membrane. This stratum of cells on the posterior surface of the cornea is not to be reckoned as an epithelium, but rather as a pseudo-epithelium or endothelium (His).‖

In the inflamed cornea of the Frog, Klebs ¶ observed a series of changes in form of the cells of the endothelium, which in some instances were quite as active as those of the lymph corpuscles, and which led to a detachment of the cells. Norris and Stricker ** likewise observed movements of the endothelial cells of Descemet's membrane in inflamed corneæ, and also claim to have seen a multiplication of the nuclei and a proliferation of the cells. If we bring a freshly-excised healthy Frog's cornea, moistened with humor aqueus as quickly as possible under the microscope, and examine the endothelium of the membrane of Descemet with exact adjustment, we shall see that it is composed of two different kinds of cells. One portion of the cells appear granular, and in them may be distinguished a round nucleus surrounded by a more or less distinct outline. Another portion of the cells, on the other hand, appear completely smooth, and without any sign of nucleus. The cells in these two conditions occur singly or united in irregular figures, and drawings of the endothelial membrane may vary considerably, owing to these different conditions of the cells and their varying distribution.

The Development of the Corneal Layers which belong to the Connective Tissue.

The histogenesis of the cornea calls for renewed researches, especially with the use of the silver and gold methods. At present we have but fragmentary observations on this subject. In the cornea of the fœtus of the Ox, $1\frac{1}{4}$ inch in length, Langhanns †† found oval or roundish cells, containing faintly-defined nuclei and lying closely together. In an embryo $1\frac{1}{2}$ inch in length the cells were found to be irregular in form, sometimes round and sometimes serrated.

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* *Mikroskopische Anatomie*, Deutsch von Kohlschütter, Leipzig, 1852, p. 393, Bd. ii., Taf. lxiii., fig. 11.

† *Archiv für Ophth.*, Bd. ii., Abth. 2, p. 48.

‡ L. c., p. 607. § L. c.

‖ *Häute und Höhlen des Körpers*, Basel, 1865, p. 18.

¶ *Centralblatt für die med. Wissenschaften*, 1864, p. 513–516.

** L. c., pp. 16 and 17. †† L. c., pp. 17 and 18.

In an embryo $2\frac{1}{2}$ inches in length a fibrous appearance may be seen in fragments of the cornea, the cells are large, and their form already resembles that of the corpuscles of the fully-developed cornea. In the fœtus of an Ox whose eye was about 6 mm. in diameter, the cells were seen to be pale, elongated, and furnished with 4–6 processes.

I have made observations on a number of eyes of the Sheep's embryo. These eyes had been hardened in Müller's fluid, and embedded in Peremeschko's mass, and the sections were stained with carmine. In these preparations I find the cornea at first to consist of round, closely-packed cells. At a later period the cells appear to be flattened in the direction of the thickness of the cornea. These flattened cells lie also closely together one above the other, like the cells in the superficial strata of a flat epithelium.

Between these flattened cells there now appears a clear substance which pushes the cells apart in the direction of the thickness of the cornea, so that we have a picture which already reminds one of a meridional section of the fully-developed cornea.

This separation of the cells does not take place simultaneously in all the layers of the cornea. It commences rather in the vicinity of the anterior pole of the eye, involves first the most anterior layers, and progresses gradually toward the anterior chamber. At a certain period of development the anterior chamber is separated from the corneal layers and their already mature intercellular substance by a layer of stratified cells, all of which are exactly like the innermost row of cells corresponding to the endothelium of Descemet's membrane. The membrane of Descemet, however, is not yet present. It makes its appearance as a narrow stripe between the innermost layer of cells and the layers of cells which lie external to this.

In the embryo of the Calf, 8 centimetres in length, and in the Human embryo of the second or third month, the membrane of Descemet is to be found, according to Donders,* with the same structureless appearance as in the adult, only it is thinner.

At a very early stage fine fibrils or fibrillar markings may be seen in the clear substance, which, as stated above, pushes apart the flattened cells of the developing corneal tissue. The cells themselves seem to be furnished with processes, which pass off in the most diverse directions to communicate with the processes of neighboring cells, but which never, as is seen by sections and preparations by teasing, are continuous with the substance of the fibrils.† The latter pass into the substance filling the interspaces of the granular protoplasm of the cells, in a manner similar to that of the fibrils of connective tissue during the development of the network.‡ The histological processes of the regeneration of corneal tissue, observed in the Rabbit after shaving off the superficial layers (Donders,§ De Gonvea),‖ and in Man after loss of substance (Donders),¶ should likewise be subjected to more thorough examination.

The External Epithelium of the Cornea.

This epithelium is a laminated, flat epithelium, 0.03 mm. in thickness in Man (Henle),** and displaying in Man and the Mammalia very much the same characteristics.

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* *Nederl. Lancet*, Aug., 1851, p. 47.

† Compare Wilckens "Ueber die Entwickelung der Hornhaut des Wirbelthierauges." *Zeitschr. für rat. Med.*, 3 R. Bd. xi., p. 167. ‡ See this text-book, p. 76.

§ Holland, *Beiträge zur Natur- und Heilkunde*, Bd. i., p. 387.

‖ *Archiv für Augen- und Ohrenheilkunde*, Bd. i., p. 119.

¶ *Nederl. Lancet*, 1848, p. 218. ** L. c., p. 605.

The most superficial strata of the external epithelium consist of flattened cells, which are arranged in manifold layers one above the other; these cells have a greater diameter in the direction of the corneal surface than the adjacent deeper cells, which, when seen in situ, that is, in sections of hardened preparations, or in detached fragments of epithelium, present a polygonal form. In preparations of epithelium which have been immersed in iodized serum, or macerated for some time in a 10 per cent. solution of common salt and then for a short time in water, these cells appear rough, finely indented, and fitted into one another by their inequalities like the serrated cells (riff- or stachel-cells).

Fig. 356.

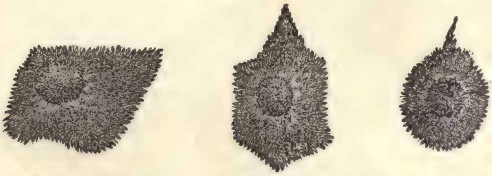

Fig. 356. Serrated cells (riff- or stachel-cells) from the middle layers of the external corneal epithelium, from the Pig. The cornea has been macerated in a 10 per cent. solution of common salt, and the cells isolated by subsequent treatment with water.

Cleland* claims to have isolated with bichromate of potash, and to have made drawings of, cells with long (fingerlike) processes, from the middle layers of the corneal epithelium of the Ox: such cells I have not been able to find even in the same animal.

The deepest layer of cells situated directly upon the corneal tissue consists of cells which are elongated in a direction perpendicular to the surface. When isolated they likewise appear rough, owing to the detachment of their serrated edges from those of the neighboring cells. They sit with broad bases upon the corneal tissue, but do not send any processes into it. The base of the cells when seen from the side appears as a brilliant border (basal border). The round nucleus of the cell lies somewhat nearer to the external than to the internal end of the cell. This may be well seen in sections of the corneæ of animals in whom the cells are particularly long, for instance, in the Ox and the Pig; the corneæ having been quickly hardened in alcohol, and the sections stained in hæmatoxylin. Krause † claims to have seen between the cells of this layer peculiar ellipsoidal cells (?) sparsely distributed.

In the Frog the epithelium, as seen at the folds of the fresh cornea, presents the appearance represented in fig. 346. Here also I am convinced that the 10 per cent. solution of salt, used until the epithelium detaches itself in shreds (Schweigger-Seidel),‡ is an excellent means of isolation.

The cells of the outermost layer form a mosaic-work, the divisions of which are marked off by brilliant lines (cell-borders, black-colored cement when treated with nitrate of silver). Each polygonal cell possesses a beautiful, sharply-defined, granular nucleus (fig. 357, *a*).

The serrated cells seldom occur in the middle layers of the epithelium of the Frog. Here the cells appear either polyhedral, with smooth angles and surfaces, or, as is often seen, they give off a limited number of longer or shorter pointed, often peculiarly-shaped processes (fig. 357, *b*).

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* On the Epithelium of the Ox. *Journal of Anat. and Phys.*, by Humphrey and Turner, vol. ii. Cambridge and London, 1868, p. 362–364.

† "Ueber das vordere Epithel der Cornea," *Göttinger gelehrte Nachrichten*, 1870, No. 8. Reichert und Du Bois *Archiv*, 1870, p. 232. ‡ L. c., p. 353.

In this case, also, the innermost layer consists of elongated cells. The length of the individual cells of this layer varies. Between shorter cells of the form *c* 1, fig. 357, are to be found longer ones of the form *c* 2, fig. 357, and owing to a diminution of the size of the inner end of the cell, we often meet with cells even more club-shaped than the one represented in *c* 3, fig. 357.

At the place where the cells come in contact with the corneal tissue they present a highly refractive border (fig. 357, *c* 1, 2, 3), which reminds of the lateral view of the smooth border sometimes seen on the surface of certain

Fig. 357.

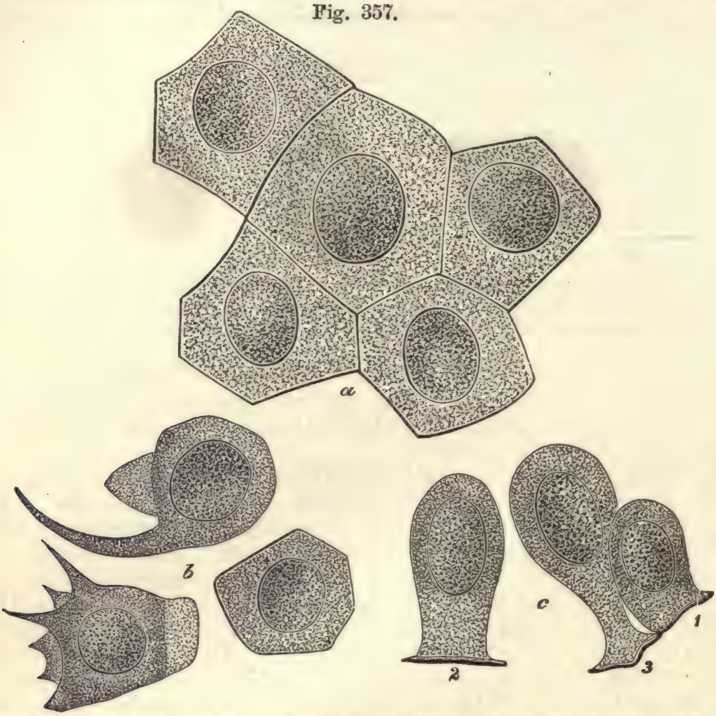

Fig. 357. External epithelium of the cornea, from the Frog. *a*, Cells from the outermost, *b*, from the middle, *c*, from the innermost layer.

conical epithelial cells. And this border, which may also be called basal border, generally appears wider than the rest of the cell; this is always the case with the club-shaped cells of the innermost layer. The widened basal borders of the cells are so joined together, or their tapering extremities are so applied to one another, that all the borders of the cells seen in situ present a brilliant line running on the margin between the epithelium and the corneal tissue. Henle* also called attention to this line, but gave another explanation of it.

I have convinced myself also that in Man and the Mammalia this line is caused by the basal borders of the innermost layer of cells.

A more exact knowledge of the corneal epithelium, in its individual layers and in the normal state, is all the more necessary, since this epithelium plays an important rôle in the experiments lately instituted on the subject of the regeneration of epithelium.

* L. c., p. 605, and fig. 459.

J. Arnold,* who began these experiments, invested them with a special signification, inasmuch as he held that, when the epithelium had been artificially removed, the deficiency was at first filled with a blastema; this, at the margins of the deficiency, was transformed into hyaline protoplasm, and this into divisions in which nuclei were developed (that is to say, into cells). But the experiments which were made on the external corneal epithelium, by Wadsworth and Eberth,† F. A. Hoffmann,‡ and by Heiberg,§ all go to disprove the blastema of Arnold. The regeneration takes place by means of new cells, which are formed by a budding and division of the marginal epithelial cells, or of cells at the edge of islands of epithelium which have been left.

F. A. Hoffmann ‖ states that he has never observed the cells of the deepest epithelial layer to be furnished with processes. This would put this layer in an anomalous position (compare Cleland ¶ and Krause, l. c., p. 235). Heiberg,** however, contradicts the statement of Hoffmann. But even Heiberg lays too little stress upon the peculiarities of the undermost layer of the intact corneal epithelium. That the cells of the middle layer, even in the normal condition, have processes, we have seen above. Heiberg †† describes slow changes in form in the buds of regenerating epithelial cells. The putting forth and withdrawal of knoblike processes had been previously observed by F. A. Hoffman,‡‡ in cells of the anterior corneal epithelium, in the vicinity of an eschar, caused by cauterization with the nitrate of silver. The regeneration of epithelium, in places where the epithelium had been removed from the central portion of the cornea, by scratching with a cataract needle (unfortunately the size of the deficiency is not given), was completed in the Frog in forty hours or longer, generally before the end of the third day, in Mammalia and Birds within the first twenty-four hours. After this length of time the defect was found to be completely repaired (Heiberg).§§

Wandering cells are to be found among the anterior corneal epithelium, as well as in the corneal tissue; also between these two tissues wandering cells have been observed (epithelial, subepithelial wandering cells, v. Recklinghausen,‖‖ Engelmann).¶¶ A participation of the wandering cells in the regeneration of lost epithelium is denied by J. Arnold,*** Wadsworth and Eberth,††† F. A. Hoffmann,‡‡‡ and Heiberg.§§§

The Nerves of the Cornea.

They enter at the margin of the cornea, at tolerably regular intervals, and in the form of trunks of various size. The fact of the entrance of medullated nerve-fibres into the cornea was long ago recognized (Schlemm,‖‖‖ Bochdalek). ¶¶¶

The number of medullated nerves entering the cornea is different in different individuals and species. In Man the number is given as 20–30 (Kölliker),**** 24–36 (Kölliker),†††† and 40–45 (Sämisch).‡‡‡‡ In the Rabbit 20–30 have been counted, in the Ox and the Sheep 10–20, in the Chicken and the Dove 12–18 (Kölliker),§§§§ in the Guinea-pig 15–18 (Cohnheim),‖‖‖‖ and

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* Virchow's *Archiv*, Bd. xlvi., p. 168. † Virchow's *Archiv*, Bd. li., p. 361.
‡ Virchow's *Archiv*, Bd. li., p. 373.
§ *Medicin. Jahrbücher der Gesellschaft der Aerzte in Wien*, 1871, p. 7.
‖ L. c., p. 388 and 389. ¶ L. c., p. 363. ** L. c., p. 19. †† L. c., p. 12.
‡‡ *Ueber Contractilitätsvorgänge im vorderen Epithel des Froschhornhaut.* Diss. inaug. Berlin, 1861. §§ L. c., p. 10. ‖‖ Virchow's *Archiv*, 28. Bd., p. 191.
¶¶ L. c., p. 15. *** L. c., p. 170. ††† L. c., p. 370. ‡‡‡ L. c., p. 384.
§§§ L. c., pp. 13 and 20. ‖‖‖ *Berliner Encyclopädie*, Bd. iv., p. 22.
¶¶¶ *Bericht über die Versammlung der Naturforscher in Prag, im Jahr* 1837. Prag, 1838, p. 182.
**** *Mikroskopische Anatomie*. II. Bd., p. 627.
†††† *Gewebelehre*, Leipzig, 1867, p. 650.
‡‡‡‡ *Beiträge zur normal. und path. Anatomie des Auges.*
§§§§ *Mikr. Anat.*, II. Bd., p. 627.
‖‖‖‖ Virchow's *Archiv*, Bd. 38, p. 354.

in the Frog 15 on an average (Kühne).* While the nerves are distributed throughout the cornea, they form a plexus, remarkable for its manifold anastomoses, and whose finer ramifications push toward the anterior surface, where they construct a nervous network, immediately under the anterior "structureless lamellæ," and close under the epithelium (Kölliker).† The nervous plexuses, formed of non-medullated fibres, exist in like manner in the cornea of Man and of the most diverse animals (His,‡ J. Arnold, § Sämisch,‖ Ciaccio,¶ Kühne),** and in the Frog the fine extremities of the nerves distributed throughout the cornea are said to communicate with the corneal corpuscles (Kühne).††

In the Mammalia, twigs of the external portion of the nervous plexus may be followed into the anterior corneal epithelium (Hoyer).‡‡ Cohnheim §§ obtained the best idea of the distribution and terminations of the corneal nerves, since in his researches he made use of the chloride of gold, which is wonderfully adapted for this purpose. The beautiful results obtained by him have been for the most part confirmed by Kölliker and Engelmann.

At a short distance from the corneal margin the medullated nerve-fibres suddenly lose their medullary sheaths. The point at which this takes place is by no means constant; often it is in the main trunk as it enters the cornea, often in its branches of the first, second, or even third degree.

The nerves, as they proceed beyond this point, consist of a greater or less, generally a very considerable number of exceedingly fine non-medullated nerve-fibres. These bundles of non-medullated fibres enclose isolated, longitudinally oval nuclei, which cannot, however, with certainty be referred to a continuous sheath. The individual fibres often exhibit very plainly a varicose appearance. These numerous fibres must obviously take their origin from a division or an unravelling of the axis-cylinder (Max Schultze).

These fibres as they penetrate the tissue of the cornea form an abundant network by manifold ramifications, by anastomoses, and repeated division of the fibrils contained in the bundles. In the deeper portions of the cornea this network is more widely meshed and composed of larger nerves (fig. 358), but toward the external surface the nerves gradually become finer and the meshes of the network smaller (fig. 358).

The plexus, as a whole, occupies by preference the external two-thirds of the thickness of the cornea, in Mammalia. In the portions of corneal tissue adjacent to the membrane of Descemet are to be found only a few isolated fibres, which branch off at the margin of the cornea from the largest nerves of the most internal divisions of the plexus, and run backwards. Kölliker claims to have followed, in the Rabbit's cornea, the finest twigs of these fibres in a horizontal course along the membrane of Descemet and at only a short distance from it.

The plexus found in the anterior portion of the cornea may be divided into several parts. As the larger nerves pass in an oblique course from the posterior to the anterior portions of the cornea, they spread out in fine ramifications, which generally run parallel to the corneal surface, and form a regular flat plexus at a short distance from the dividing line between corneal tissue and epithelium (just beneath the anterior limiting layer). From

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* *Untersuchungen über das Protoplasma*, etc., Leipzig, 1864, p. 133.
† L. c., p. 627.
‡ *Beiträge zur normal. und path. Anatomie der Cornea*, p. 60.
§ *Bindehaut der Hornhaut.* ‖ L. c.
¶ *Quarterly Journal of Microscop. Science*, 1863, July, p. 177.
** L. c. †† L. c.
‡‡ Reichert and Du Bois, *Archiv*, 1866, p. 180. §§ L. c., p. 343.

this plexus arise fine branches (rami perforantes) which take a perpendicular or somewhat inclined course toward the margin between corneal tissue and epithelium; arrived at a point just beneath the external epithelium, they are resolved into a series of finer twigs, which diverge pencil-like (Guinea-pig) (Cohnheim) or in the stellate form, thus constructing another exceedingly delicate flat plexus, the subepithelial plexus (fig. 359). From this again fine twigs push forward at pretty regular intervals between the

Fig. 358.

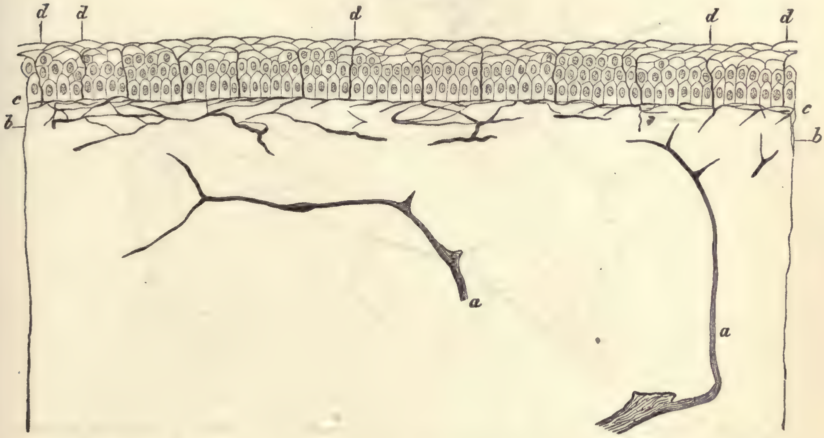

Fig. 358. Corneal nerves from the Pig: the cornea has been treated with chloride of gold, and the section made perpendicular to the surface. *a a*, Larger nerves; *b b*, plexus beneath the anterior limiting layer of corneal tissue; *c c*, subepithelial plexus; *d d d d d*, terminal twigs ascending through the epithelium.

deeper elongated cells and the more superficial .ound cells of the epithelium. During this course they preserve a direction perpendicular to the surface: only when they have reached the internal layer of the superficial, flattened cells they send off in all directions the finest terminal twigs, which, after dividing once or more, terminate often somewhat swollen in the most superficial layer of epithelium. When viewed from the surface the ends of these ascending fibres correspond to the nodal points where the converging terminal twigs unite. I have in no case been able to convince myself that an anastomosis existed between the terminal twigs of different nodal points. Stricker recently showed me in the cornea of the Rabbit a fine plexus, first demonstrated by S. H. Chapman, which was supposed to be situated on the surface of the external epithelium.

The above statements are for the most part based upon results obtained from the cornea of the Pig and the Ox, when treated with the chloride of gold. The appearances are, however, with but slight exceptions, the same in the other Mammalia that have been examined.

The cornea of the Frog may likewise be used for making beautiful gold preparations (fig. 360); and it has also this advantage, that after the removal of the epithelium it may be placed in toto under the microscope, while the thicker corneæ of the above-mentioned animals must be cut into meridional and surface sections after the impregnation with gold and the reduction of the same.

The nervous distribution of the Frog's cornea has been followed by Kühne,* and even more thoroughly by Engelmann, in the fresh cornea moistened with humor aqueus.

Fig. 359.

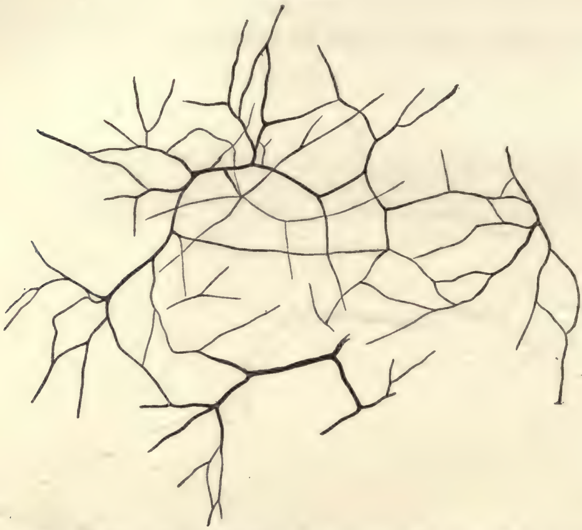

Fig. 359. Portion of the subepithelial nervous plexus, from the Pig's cornea, treated with the chloride of gold.

Nervous trunks (5–15 in number, or even more) composed of medullated fibres cross the margin of the cornea at 6–8 points. Besides this, medullated nerve fibres, isolated or in pairs, enter the cornea at various other points. The greater number of these fibres run at first for 0.2–0.5 mm. in a straight line towards the centre of the cornea; only a few diverge at the corneal margin, forming a right angle with the main trunk, taking a course at first parallel to the margin and afterwards towards the centre.

As a rule the nerves lose their medullary sheaths at a short distance from the corneal margin (0.3–0.5 mm.), and then by repeated dichotomous divisions form an abundant widely-meshed plexus, which lies nearer the posterior than the anterior surface of the cornea. Real anastomoses are no more demonstrable in this plexus than in that of the Mammalia. Sheaths are indicated on the medullated as well as the non-medullated fibres by oval nuclei which follow the distribution of the nerves. These nuclei become more infrequent in the smaller subdivisions of the nerves, and finally are to be found only in the nodal points of the plexus, to which they give the appearance of being somewhat thickened. Thus we may have an appearance resembling ganglion cells, such as is likewise seen in the corneal nerves of Mammalia. But real ganglion cells do not exist in the nodal points of the nervous plexus either of the Frog or of Mammalia.

The above-mentioned plexus, situated as it is almost in a single plane of the cornea, gives off at many points branches, which form a dense lattice-

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* *Untersuchungen über das Protoplasma*, etc., p. 132.

† L. c., p. 15.

like nervous expansion in the corneal tissue both behind and in front of (as far as the edge of the anterior third) the coarser plexus. Also in this lattice-work the existence of real anastomoses is doubtful; here also occasional nuclei may be found, situated at the nodal points of the finest bundles, but no true ganglionic enlargement. The finest threads are gradually lost in the corneal tissue, leaving it impossible to form an opinion as to the manner of their termination. The network just described has been called by Engelmann* the nervous distribution of the true corneal tissue, in contradistinc-

Fig. 360.

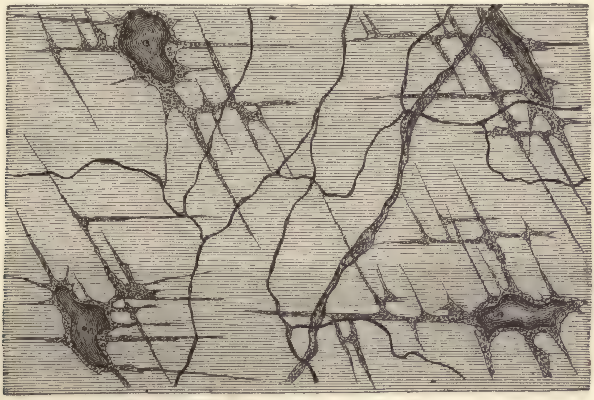

Fig. 360. Portion of Frog's cornea treated with chloride of gold. *n n n n*, nerves.

tion from the nerves of the corneal epithelium.† These latter are branches of the earlier-described larger network, and ascend abruptly through the corneal tissue toward the external epithelium. They are joined by occasional fine non-medullated fibres which pass directly forward from the lateral margin toward the epithelium : the number of all these nerves is 40–60 in each cornea. At the boundary-line between corneal tissue and external epithelium these nerves give off a varying number of branches, which run in various directions parallel to the surface of the cornea, and finally, some being undivided and others after repeated divisions, pass between the long cells of the deepest layer of epithelium : thus is formed at this point another dense plexus, whose terminal twigs ascend between the cells lying just beneath the flat cells of the epithelium. All the appearances just described may be most beautifully seen in successful gold preparations. I have never observed the terminal fibrils in the Frog to pass through the flat cells of the epithelium. A communication of the above-described corneal nerves with the corneal corpuscles (Kühne) does not exist (Engelmann).

I have always in vain sought in otherwise excellent gold preparations for the fine straight lines, drawn by Lipmann‡ between the finest nerve fibres of the cornea and the nucleoli of the corneal corpuscles, as well as for the straight lines described as arising from the nucleoli of the endothelial cells of the membrane of Descemet. Judging from these gold preparations, I must on the contrary hold that the finest nerve fibres of the corneal tissue

* L. c., p. 17. † L. c., p. 19.
* Virchow's *Archiv*, Bd. 38, p. 218; Taf. vii., fig. 1–6.

are always seen to pass by the corneal corpuscles and their processes, and therefore it is impossible to demonstrate a connection between the corneal corpuscles and the nerves.

The Margin of the Cornea (Corneal Groove, Limbus Corneæ).

The margin of the cornea is interesting on account of the transitions and connections of the already-described corneal layers at that point.

The external epithelium *aa′*, fig. 361, passes over without interruption into the epithelium of the conjunctiva. We often find the external epithelium with the anterior limiting layer of the corneal tissue (lamina elastica anterior) very improperly designated as conjunctiva corneæ (in Kölliker* for example). The anterior limiting layer, however, neither agrees in structure with the peculiar tissue of the conjunctiva bulbi, nor is there any continuity of fibres between the two. The stroma of the conjunctiva, *kk*, fig. 361, terminates in a wedge-shaped edge between the epithelium and the corneal tissue. The latter, *bb′*, fig. 361, is continuous with the sclerotic,

Fig. 361.

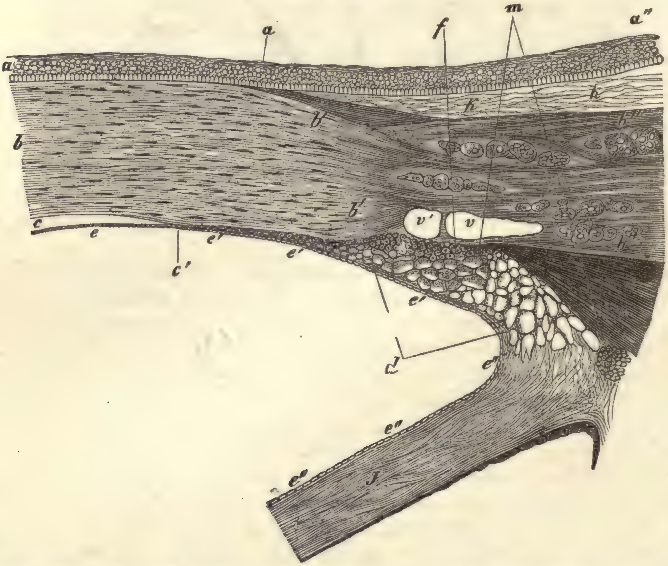

Fig. 361. Corneal margin, from a meridional section of the Human eye. *aa′*, External epithelium of the cornea; *a′a″*, epithelium of the conjunctiva bulbi; *bb′b′*, corneal tissue; *b′b′b″b″*, sclerotica; *kk*, conjunctiva; *vv′*, canal of Schlemm; *cc′*, membrane of Descemet; *d*, process of the iris; *J*, iris; *e*, endothelium of the membrane of Descemet; *e′e′e′*, of the ligamentum pectinatum iridis; *e″e″e″*, of the iris; *f*, meshwork of the space of Fontana; *m*, musculus ciliaris.

and in Man the external portions of the sclera project further toward the centre of the cornea than the middle and internal portions, and the latter more than the middle portions; so that in a meridional section the margin, where the transparent cornea is separated from the untransparent sclera,

* *Handbuch*. Leipzig, 1867, p. 647.

describes a curved line (fig. 361). It is very difficult to arrive at a clear understanding of the relations of the corneal tissue to the connective tissue of the sclerotica.

In preparations of sections both kinds of fibres are apparently continuous with one another without interruption, and in preparations made by tearing up the tissues with needles the appearances are similar. But, owing to the extraordinary fineness both of the corneal and scleral fibrils, these appearances are not worthy of too much trust. Even if there were no continuity between the two kinds of fibres it would be very difficult to separate them, and to obtain a view of their natural terminations.

To me it seems probable that these tissues are only intimately fitted one into the other. If we spread apart the corneal tissue with injection by puncture, as above described, as far as the limbus, and extract again the injection, we shall see that the thin laminæ of the sponge-like corneal tissue are fitted in with the layers of the compact sclerotic tissue.

But above all, the chemical differences of the corneal tissue and the connective tissue render a direct continuity of fibre improbable. Sections of the membranous capsule of the eyeball, which has been boiled in vinegar or dried, are admirably adapted for double staining with carmine and picric acid (Schwarz*), and in such preparations we may see that the cornea is stained yellow, while the sclerotic, like all connective tissue, is stained red; in the cornea the corpuscles alone have a red color.

The membrane of Descemet, cc', fig. 361, tapers off to a point at its margin c', and in Man this takes place at a considerable distance from the angle of the anterior chamber. It does not, however, terminate here abruptly, but is in connection with peculiar fibres (Henle),† which, arising by larger or smaller bases from the membrane of Descemet, take at first an irregular and intricate course (Schwalbe),‡ and finally form an annular zone at the margin of the membrane of Descemet (Iwanoff and Rollett),§ bounded externally from the very beginning by the tapering end of the latter. The processes of the iris, fig. 361 d (Iwanoff and Rollett)‖ are continuous (Schwalbe)¶ with this marginal ring (Schwalbe)** of the membrane of Descemet, and so also the most anterior trabeculæ of the network of the space of Fontana, fig. 361 f, in short, the so-called ligamentum pectinatum iridis of Hueck. The same relations exist in the Ox and the Pig as in Man. In the Dog, on the contrary, the marginal ring of the membrane of Descemet is wanting, and the processes of the iris are developed directly from conical fibrous offshoots of the membrane of Descemet, the bases of which describe tortuous markings (Schwalbe).††

The endothelium is uninterruptedly continuous with the endothelium of the processes of the iris, also with that of the most anterior trabeculæ of the space of Fontana, $e'e'$, and thus ultimately with that of the anterior surface of the iris, $e''e''$, fig. 361 (Iwanoff and Rollett),‡‡ (Schwalbe).§§

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* *Sitzungsberichte der Wiener Akademie*, Bd. 55, 1. Abth., p. 676.

† L. c., pp. 607 and 626.

‡ *Archiv für mikroskopische Anatomie*, Bd. 6, p. 278.

§ *Archiv für Ophth.*, Bd. xv., 1, p. 49.

‖ L. c., p. 19, 36, 44.

¶ L. c., p. 276–280.

** L. c.

†† L. c., p. 279.

‡‡ L. c., p. 39–43, 49.

§§ L. c., p. 283.

VIII. CONJUNCTIVA AND SCLEROTICA.

For the present treatise I was in possession of a manuscript by Stieda. This had been submitted to me about two years ago, at a time, therefore, when the author could not have been informed of the plan according to which the special chapters of this work were to be treated. I ascertained too late that the treatise in hand was much too limited for our purpose. In order, therefore, that the appearance of our last number should not be still further delayed, I have myself undertaken the task of making it several times longer than its original dimensions. In this work I have been for the most part only a compilator.

The illustrations are taken from preparations by E. Klein; and for the rest, besides the manuscript of Stieda, I have made use of a manuscript prepared for this purpose by E. Klein, the text-books of Henle, Kölliker, Leydig, the monograph by Brücke, and the essays of Schmid and Helfreich. From the four last-named authors I have quoted literally with the use of quotation-marks. Only with reference to the nerves have I instituted some original work, and that by the hands of a pupil: this work, as the reader will find, was almost without result.—S. STRICKER.

WE may distinguish two divisions of the superior and inferior eyelid. The one nearer the edge of the lid is supported by a firm plate, the tarsus, while the other division, nearer the bony edge of the orbit, is devoid of any such support. Henle calls the one "tarsal portion," the other, "orbital portion" of the eyelid.

Each of these lids is composed of an external layer of skin, an internal layer of mucous membrane, and a middle layer, in which are situated the muscular fibres of the orbiculus palpebrarum, and the tarsus.

The external layer of skin is a prolongation of the integument of the face, which at the free edge of the lid is continuous with the layer of mucous membrane. This latter lines the internal surface of the lid as far as the bony edge of the orbit, where it is reflected upon the eyeball, upon the anterior surface of which it may be followed up to the margin of the cornea.

As long as the mucous membrane is applied to the lids it is called conjunctiva palpebrarum; the place where it is reflected upon the globe is designated as fornix conjunctivæ, and finally the portion which covers the eyeball is called conjunctiva bulbi. At the inner angle of the eye the conjunctiva forms a fold, the plica semilunaris, which is regarded as the rudiment of a third eyelid or nictitating membrane. Heinrich Müller found smooth muscular fibres in this fold, and these also are regarded as rudiments of a nictitating muscle.

Leydig* found that the hard plate in the nictitating membrane of domestic animals consisted of true cartilage, and Harrison made the same observation with regard to this membrane in the Elephant.

In the Batrachia the nictitating membrane is peculiar both in structure and its optical relations. In the (fresh) living state it is so transparent that when spread out in aqueous humor or blood serum immediately after excision it may be examined with the highest powers. Especially if we cut off the thick margins there remains a perfectly even piece, peculiarly fitted for examination with the highest powers.

In such preparations one may have the opportunity of examining in the fresh state epithelium, connective tissue, blood-vessels, nerves, and glandular structure. Above all, the fresh blood-vessels are here exhibited with an

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* *Lehrbuch der Histologie*, 1857.

elegance such as no known organ of the adult animal presents after its separation from the living body. Moreover, the opportunity is here offered of examining in detail the simple flask-shaped glands, with their excretory ducts, passing through the external epithelium. Finally, the medullated nerve-fibres, isolated or united in bundles, may be observed in a state at least not far removed from that of life.

Stricker several years ago noticed spontaneons contractions in the capillary blood-vessels of such nictitating membranes. But this observation has not as yet been confirmed.

The integument both of the upper and under lid of Man is thinner than the integument of the face, and is freely movable upon the subjacent tissues. The epidermis consists of only a thin layer of horny epithelium, and a rete Malpighii composed of several layers of polyhedral cells. The corium contains papillæ enclosing vascular loops, which in the new-born Child are but small and irregular, while in the Adult they are distinct and well developed. The corium consists of loose fibrillar connective tissue, in whose anterior layers many branching cells are present, and is deficient in elastic fibres.

Fig. 362.

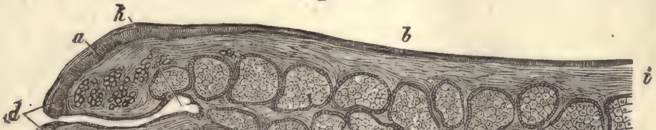

Fig. 362. Perpendicular section through the lid of a new-born Child. (Hartnack, Oc. 3, Ob. 2.) *a*, Epithelium of the free margin of the lid ; *b*, epithelium of the conj. palpebrarum ; *c*, epidermis of integument of lid ; *d*, portio Riolani ; *e*, cilia ; *f*, cutis ; *g*, musc. sphincter orbic. ; *h*, Meibomian gland ; *i*, conjunctival tissue between Meibomian gland and epithelium ; *k*, excretory duct of Meibomian gland ; *l*, hair-follicle ; *m*, sebaceous follicle ; *n*, sweat-gland.

The subcutaneous tissue consists of a superficial dense, and a deeper, less dense layer of fibrous tissue. The deeper layers contain but few fat-cells in the vicinity of the margin of the orbit.

The external integument continues to a point not far from the middle of the margin of the lid, which is about 2 mm. in breadth : at this point, how-

ever, the rete Malpighii is more extensive and the papillæ of the corium are more numerous and more extensive than on the anterior surface of the lid.

The integument of the eyelids possesses hairs and glands.

The hairs are larger in the new-born Infant than in the Adult, in whom they are scarce and very small. The hair-follicles, and their accompanying sebaceous follicles, take root in the superficial denser layer of the subcutaneous tissue.

The eyelashes are small and curved, and are inserted into the integument of the margin of the lid in two to four rows. Their circular muscular layer is very strongly developed, especially in the deeper portion of the hair-follicle. A sebaceous follicle always opens into the neck of the hair-follicle.

According to researches by Moll, the length of life of the cilia is about 100 days. Owing, therefore, to a rapid change of hairs, we generally find at the margin of the lid hairs in several stages of development.

Fig. 363.

Fig. 363. Longitudinal section through the root of an eyelash of the new-born Infant. (Hartnack, Oc. 3, Obj. 7.) *a*, Papilla of the hair; *b*, longitudinal fibrous envelope of the hair-follicle; *c*, striated muscular fibres; *d*, vitreous membrane of the hair-follicle; *e*, cells of the external sheath of the root; *f*, layer of cells covering the vitreous membrane of the papilla; *g*, circular muscular envelope of the hair-follicle.

Besides the change of hairs, which proceeds in the usual manner as already described in this work, a formation of new hairs also takes place independently of already existing hair-follicles, by direct involution of the rete Malpighii.

The sweat glands of the integument of the lids are small, roundish bodies, which consist of a tube convoluted so as to form a coil: a short excretory duct ascends in a pretty direct course from the coil, and, perforating the epidermis, opens upon the surface. Since the layer of epidermis is very thin, the spiral course of the duct is here scarcely to be remarked.

In the inferior portion of the skin of the lid the sweat-glands are of a very peculiar form. Each gland presents the appearance of a cylindrical canal, which commences as a blind tube and takes a slightly tortuous course. While the other glands stand perpendicular to the surface of the skin, and therefore, owing to the thinness of the skin at this point, must be exceedingly small, the glands just mentioned of the inferior portion are considerably larger. They take a course parallel to the surface of the skin, and their blind extremities are situated far above, between the anterior and middle lamellæ of the lid, while the ducts open at a short distance from the margin of the lid.

Transverse sections of these glandular tubes display a circular lumen possessing an envelope of connective tissue, sometimes with longitudinal muscular fibres, and lined with a layer of cells. These cells are a continuation of the rete Malpighii; somewhat deeper they are replaced by cylindrical cells, which, in the new-born Infant, reach to the

bottom of the follicle, but which in the Adult, both in the deepest and the less dense layers of the subcutaneous tissue, give place to cubic cells: these cells sometimes contain a yellowish-brown pigment. In the vicinity of its mouth the canal diminishes somewhat in calibre, and opens with a funnel-shaped orifice, generally into the follicle of an eyelash, but occasionally separately. The cellular lining of the canal is gradually continuous with the cells of the epidermis. This variety of sweat-gland was first minutely described by Moll.*

The connective-tissue bundles of the deeper, looser portion of the subcutaneous tissue form, by interweaving with the connective-tissue trabeculæ of the analogous portion of the submucous tissue, a network lying near the middle of the eyelid, in the interstices of which are embedded the fasciculi of the musculus sphincter orbicularis, which runs parallel to the edge of the lid. These fasciculi are arranged one above the other, and extend from the orbital edge to the free margin of the lid, so that the last fasciculi, the uppermost one of the inferior lid and the lowest one of the superior lid, are situated between the roots of the most anterior cilia and the skin of the anterior surface of the lid.

A few fibres branch off from these last bundles, some of which pass between the cilia and some toward the anterior edge of the lid.

Besides this muscle, there is also the so-called musculus ciliaris Riolani. This almost always consists of two portions, both of which run parallel to, and near the edge of the lid. The larger portion of it, in fact a large muscle, lies between the most posterior cilia and the orifices of the Meibomian glands, while the smaller portion, consisting of 3–5 smaller fasciculi, is embedded close to the posterior edge of the lid, between the mucosa of the conjunctiva and the neck of the ducts of the Meibomian glands.

The network traversed by the bundles of these two portions, and in whose interstices each striated muscular fibre lies, is in the new-born Infant a very delicate plexus of branching nucleated cells.

The Meibomian glands number 30–40 in the upper and 20–30 in the under lid. They are embedded in a dense mass situated between the middle and posterior layers of the lid: this mass may be separated by dissection from the other portions of the lid, and is generally called the tarsus, or the tarsal cartilage. In sections it is plain that the so-called tarsus is continuous with the connective-tissue substratum of the middle and posterior layers of the lid, and is distinguishable from the surrounding tissues only by the peculiar arrangement and appearance of its elements. The tissue of the tarsus consists of more or less regularly arranged connective-tissue bundles, whose fibres are broader, more brilliant, and more resistant to reagents than the ordinary fibrillar connective tissue. In the immediate vicinity of the glands the bundles run horizontally from before backwards, and at the same time encircle the individual acini in larger or smaller curves, weaving about them, as it were: here and there a few fibres run diagonally, crossing one another. In the neighborhood of the muscular layer on the one hand and the conjunctiva on the other hand, the bundles take an entirely opposite course; they run, in fact, parallel to the surface of the lid, in a direction from above directly downwards throughout the superficial extent of the lid. Between the fibres, or attached to certain of them, lie scattered not very numerous elongated nuclei, with pointed ends. Cartilage cells have not as yet been found here. The transition of the tarsal connective tissue into the connective tissue of the adjacent layers takes place gradually, the

* *Bydragen tot de nat. der oagleden*, Utrecht, 1857.

ordinary fibrillar connective tissue being replaced by the stiff fibres of the tarsus.

The Meibomian glands are arranged in rows parallel to the surface, and in such a way that their ducts open on the free margin near the posterior rim of the lid, while their distal extremities reach almost to the dividing line between the conjunctiva palpebræ and the fornix conjunctivæ. Each Meibomian gland consists of a relatively wide excretory duct, on all sides of which are arranged short, knob-like, distended acini. The duct is narrowest in the vicinity of the funnel-shaped orifice—the neck of the duct—and towards the bottom of the gland displays manifold dilatations, or acini. Each acinus is a globular or egg-shaped structure, which seems filled with cells even up to its outlet. There are many places in a gland where two or three small adjacent acini do not empty independently into the main duct, but join to form one common outlet, which opens into the main duct. In these cases the main duct seems to be considerably enlarged.

The epithelium of the main duct is a laminated pavement epithelium, and in the more superficial portions of the gland consists of one or two rows of flattened cells with oblong nuclei; then follows a single row, or two rows of polyhedral cells with roundish nuclei, and finally, lying directly upon the membrana propria, there is a layer of obliquely-placed cylindrical or cubic cellular structures, which in the fresh state are granular, and may be deeply stained by carmine or the chloride of gold.

Fig. 364.

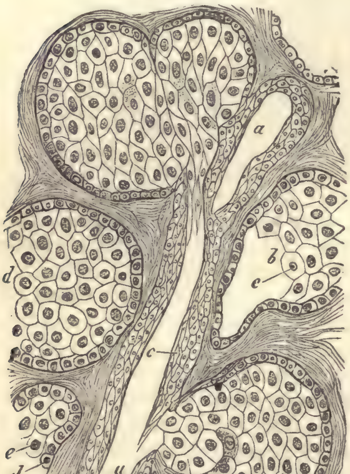

Fig. 364. Longitudinal section through a portion of the Meibomian gland, from the new-born Infant. (Hartnack. Oc. 3, Obj. 8.) *a*, Excretory duct; *b*, acini; *c*, laminated epithelium of the duct; *d*, layer of cubic epithelial cells lining the membrana propria; *e*, fatty epithelial cells of the acini.

The deepest epithelial layer, consisting of cubic or cylindrical cells, and the most superficial layer of flattened cells, are prolonged into the outlets of the individual acini. In each acinus we distinguish a membrana propria, which is sometimes structureless, and sometimes provided with a network of flat, branching structures (as seen in preparations treated with the chloride of gold). The membrana propria is covered with a layer of granular, cubic, or short cylindrical cells, which are easily and deeply tinged with coloring fluids, and contain roundish nuclei. This cellular layer is seen to be a direct continuation of the deepest layer of epithelial cells of the excretory duct. The interior of the acinus is filled with sharply-defined cells, whose edges are flattened, and which increase in size towards the centre of the acinus; in the fresh state these cells appear to be equably filled with a highly-refractive substance (fat). In preparations which have been treated with absolute alcohol and clove oil, and mounted in damar varnish, each one of these structures displays a sharply-defined nucleus, and in some cases also an exceedingly delicate network in its interior.

In the vicinity of the fornix conjunctivæ, and in that portion of the sub-

mucous tissue which has been designated as the tarsus, there are also situated some very tortuous glandular tubes, whose function is probably that of secreting mucus.

The tube itself is lined by a membrana propria upon which lies, as a rule, but a single row of granular, cylindrical cells: sometimes two rows of small pavement epithelial cells are to be found. The short excretory duct of the

Fig. 365.

Fig. 365. Section through that portion of the tarsus in which the tubular glands are situated. (Hartnack, Oc. 3, Obj. 8.) Prepared with the chloride of gold. *a*, cellular network of the tarsus; *b*, tubular glands; *c*, epithelium of the gland.

gland exhibits the same structure, and perforates obliquely the mucous membrane of the conjunctiva to open into the conjunctival sac.

These glands probably correspond to the racemose mucous glands described by Krause and Sappey as existing at the point of transition from conjunctiva palpebrarum to the fornix.

The posterior layer of the eyelid, the conjunctiva, in the fresh state appears slightly red in color, and velvet-like in texture: it is not everywhere equally thick, but increases gradually in thickness in passing from the margin of the lid, and becomes thinner again at the point of reflection upon the eyeball. The conjunctiva is not smooth, but is traversed in every direction by groove-like depressions. These sometimes deep, sometimes shallow furrows and grooves, which traverse the tissue of the conjunctiva in a straight or oblique course, cross each other and divide in such a way as to form numbers of irregularly-shaped islands, which have been described by the authors as papillæ or papilliform elevations. These furrows, however, do not everywhere form a continuous network, but appear to be completely isolated from one another in the form of groove- or gutter-like depressions. Near the edge of the lid these furrows are numerous but shallow; further above they become deeper, and at the palpebral fold they pass over without any well-defined limit into the depressions between the longitudinal folds, which give to this portion of the conjunctiva its wrinkled appearance.

But besides this, true papillæ also exist in the conjunctiva. In the new-born Infant vascular papillæ are only to be found in the vicinity of the fornix conjunctivæ, but with the adult the case is different. Here small isolated papillæ are to be found, even at a short distance from the margin of the lid, and these increase in height and breadth as we approach the fornix. Where the conjunctiva of the lid possesses no papillæ, a dense plexus of uncommonly large capillaries lies spread out just under the epithelium, but at those points where papillæ are to be found, a single loop for each papilla arises from the superficial capillary plexus.

The epithelium of the conjunctiva is laminated; it is most fully developed on the posterior half of the free border of the lid; from the posterior edge of the lid it suddenly diminishes in thickness, so that the epithelium of the posterior surface of the eyelid consists of a single superficial layer of very flat cells, each of which contains one flattened oblong nucleus, then two or three middle layers of polyhedral, and a bottom layer of cylindrical cells.

The very thin and delicate conjunctival mucous membrane of the lid consists of a basis substance of loose connective tissue, in which but a few elastic fibres may be found. The mucous membrane, however, is exceedingly rich in anastomising cells, which form a beautiful network beneath the epithelium.

I borrow the following statements with regard to the lymph follicles of the conjunctiva from a treatise on this subject recently issued by Schmid.* Bruch, in an appendix to a description of Peyer's patches in the small intestine, first mentioned similar structures on the conjunctiva of the inferior eyelid of the Ox. He described them as closed, macroscopically visible follicles, the pulpa of which was traversed by a capillary plexus of blood-vessels. These follicles were called the aggregate glands of Bruch. Stromeyer described closed follicles in the conjunctiva of domestic and wild animals. The follicles are said to be most abundant at the internal angle of the eye, and situated under the membrana nictitans, but particularly well developed on the upper lid. He describes them as pathological formations, owing to the irregularity and inconstancy of their appearance, and owing to the roughness and morbid appearances produced by them, as, for example, the injection which is prolonged even to the vessels of the bulbus. Henle designated them as trachoma glands. W. Krause found lymph follicles also in the Rabbit, the Fox, and in Birds. He first made mention of their constant occurrence, and held them to be physiological formations.

Kleinschmidt found such follicles in the conjunctiva of Man and the domestic animals. Huguenin (under Frey's leadership) expressed a similar opinion. He found the meshes of the network of connective tissue at the periphery of the follicle to be narrower and more irregular, and the trabeculæ thicker; at the centre, on the other hand, the meshes were larger, and the trabeculæ thinner. The tissue lying between the follicles was interspersed with lymph cells. In this tissue, lymphatics make their appearance in the form of long, oval spaces, without a trace of vessel-wall. Injection of the vessels brought to view an abundant system of ramifications in the interfollicular substance; the follicles are surrounded by arterial vessels, but the envelopes of the follicles are poor in blood-vessels.

Blumberg (under the guidance of Stieda) states that in the Pig the mucous membrane of the conjunctiva, with the exception of the tarsal portion, consists of adenoid tissue and possesses trachoma follicles; these were,

* *Lymphfollikel der Bindehaut des Auges.* Braumüller, Wien, 1870. In this volume may also be found a review of the literature on this subject.

however, absent in young Pigs. In the Dog, the basis substance of the mucous membrane, as well as that of the conjunctival cul-de-sac, was said to consist of adenoid tissue; in the tarsal conjunctiva the reticular tissue contained but a small number of lymph cells. In the mucous membrane of the membrana nictitans, even on its external surface, the trachoma follicles were found to be numerous, while on the tarsus the trachoma follicles occurred only occasionally in large numbers: in the retrotarsal fold the follicles were to be found with a gradual transition of the surrounding adenoid tissue into that of the follicle: in the conjunctiva bulbi the trachoma follicles were often to be found. In the newly-born Dog neither adenoid tissue nor trachoma follicles were to be found. The case was the same with the Rabbit, the Horse, and the Ox; but in the Cat the basis substance is said to consist of fibrillar connective tissue, and to contain no trachoma follicles. Finally, also Wolfring, like Stromeyer and Blumberg, considers the lymph follicles of the conjunctiva to be pathological formations.

Schmid now made his researches on Dogs, Pigs, Sheep, and Children at various ages, beginning with the first week of life; also on Cats, Rats, and Otters in the adult state. He found that in the animals just mentioned the follicles were generally found at the inner angle of the eye, and at the angle of reflection of the conjunctiva of the third eyelid upon the globe. In order to render the follicles plainly visible to the naked eye he macerated the preparation in a half per cent. solution of hydrochloric acid.

He was unable to find any follicles in animals less than a week old. The tissue of the conjunctiva palpebrarum and of the retrotarsal fold is a diffuse adenoid tissue: the conjunctiva bulbi partakes of this form only very slightly, namely, at the angle of reflection upon the tarsus.

In the second week of life a richer distribution of vessels and a more abundant collection of cells is to be met with at certain points. Bundles of connective tissue, of peculiar arrangement, with large blood-vessels, surround these places, whose external form is rendered more conspicuous by an indentation of the epithelial surface or of the submucous tissue. The follicle is formed at the end of the third week.

The structural conditions described by Schmid show that we here, in fact, have to do with formations similar in every respect to the lymph follicles.

It remains, therefore, only to mention what is said concerning the lymphatics. Schmid made use of the injection by simple puncture with the hand syringe. The immediate vicinity of the limbus is recommended as the place best fitted for this procedure.

In the entire conjunctiva he found, as Teichmann had already demonstrated with regard to the limbus conjunctivæ of Man, a superficial and a deeper plexus of lymphatics, which communicate with one another by manifold anastomoses. The lymphatics of the limbus are connected with those of the rest of the conjunctiva only by scanty anastomoses. The superficial plexus is distinguished by smaller and finer channels, which have a very regular boundary. We may often see given off from them short lateral processes, which are sometimes more pointed and sometimes relatively broader, and which terminate in blind extremities. The more deeply situated lymphatics are on the contrary broader, with more uneven boundary, and often present the characteristic valvular arrangement. In general it may be stated that the limbus conjunctivæ presents a very finely-meshed plexus, that the anastomoses, especially of the superficial layer of the bulbar conjunctiva, are more infrequent, while, on the other hand, the

retrotarsal fold as well as the lids present again more dense and more abundant anastomoses.

The conjunctiva is reflected from the lid upon the anterior surface of the bulbus as a thin membrane attached by very loose tissue to its surroundings, and thus forms that division of the conjunctiva which is known as fornix conjunctivæ. The epithelium which covers this portion of the conjunctival sac differs in many respects from the epithelium of the tarsal conjunctiva. It consists of 2–4 layers: the topmost cells are conical or cylindrical, while the following layers are composed of polyhedral or small roundish cells. The mucous membrane possesses no well-marked papillæ, and differs but little from that of the lid; it is rich in elastic fibres, also in ramifying cells, and superficial plexuses of wide capillaries.

Concerning the conjunctiva bulbi we have only to mention that it is covered by a laminated pavement epithelium, which consists of the same layers as the epithelium of the free margin of the lid; the surface of the mucous membrane is not smooth, but exhibits isolated, well-developed papillæ, which diminish in size and number toward the cornea, and in its immediate vicinity disappear altogether. The epithelium also decreases in thickness toward the corneal margin, reaching at that point its minimum of thickness.

The epithelium of the cornea is a direct continuation of the epithelium of the conjunctiva bulbi, but the following points of difference may be noticed between the two. The cells in the deepest and middle layers of the corneal epithelium are more sharply defined, and at the same time more transparent than those of the conjunctiva bulbi. In many animals dark pigment granules are to be found in the vicinity of the corneal margin within the nuclei, and within the cell bodies of the epithelium of the above-mentioned layers of the conjunctiva bulbi.

Fig. 366.

Fig. 366. *a*, Epithelium of the conjunctiva of the margin of the eyelid; *b*, epithelium of the conjunctiva bulbi; *c*, epithelium of the conjunctiva palpebrarum; *d*, epithelium of the fornix conj. From perpendicular sections of preparations, treated with the chloride of gold. (Hartnack, Oc. 3, Obj. 8.)

Concerning the nerves of the conjunctiva, the views held at the present time will be found in the following extract from a work by Helfreich.*

"We are indebted to W. Krause† for the first communication on the details of the distribution of the conjunctival nerves. According to his description, the nerves supplying the conjunctiva pass gradually into the superior layer of the propria after manifold interweaving and interchange of fibres, and finally end in terminal organs called by him terminal corpuscles: in these he distinguishes a nucleated envelope of connective tissue, and an inner corpuscle of finely granular substance of low refractive power, in the middle of which lies a pale terminal fibre with a somewhat club-shaped extremity. Krause, however, was successful in finding this

* Würzburg, 1869.

† *Ueber terminale Körperchen*, 1860.

terminal apparatus in but few animals besides Man, namely, in the Horse, the Ox, the Sheep, and the Pig; and even in these animals their number was relatively small, and their distribution in a great degree unequal and irregular. He states that sometimes one may search over considerable ground without finding a single one of these terminal corpuscles, while in other places a dense collection of them may be found in connection with the radial distribution of but few fibres. He did not attempt to count them, owing to the peculiar difficulties in so doing, but after making an estimate gives it as his opinion that the number of terminal corpuscles in the conjunctiva is probably uniform in the various animals, as for instance in Man; and also that a strikingly less number of nervous terminal apparatuses are to be found in the conjunctiva than in the skin of the last phalanx of the finger. The form of the terminal corpuscle in Man, as in different animals, is various. In Man, as in the Ape, they are roundish, almost globular; in other animals they have in general a lengthened oval, or distinctly cylindrical contour; at the same time they are either straight or slightly curved. In regard to their size, Krause says that it is generally in direct proportion to the size of the animal, increasing with the size of the body, while in very young animals they have the same character as in the adult, but a somewhat less extent. With respect to their minuter structure, the envelope of the corpuscle is said to consist of delicate connective tissue, which is continuous with the neurilemma of the corresponding double-contoured nerve-fibre, and in which are to be found many nuclei, generally elongated in form. The inner corpuscle, the largest portion of the entire organ, is of finely granular character, and in its substance is embedded the terminal fibre which represents the end of the double-contoured fibre. The terminal fibre generally ends before reaching the anterior limit of the inner corpuscle in a slight knob-like enlargement. In the inner substance of the terminal corpuscles of Man there are generally to be found a number of terminal fibres, which take a somewhat tortuous course, and which, in most cases, arise from a single nerve fibre.

The statement of Krause, founded upon these researches, that these terminal corpuscles constituted the only method of termination of the conjunctival nerves, has been vigorously contested by J. Arnold.* The latter, in the first place, declared that the terminal corpuscles of Krause are not original formations but artificial products, and ascribed their existence to the method employed by Krause; he also described a pale plexus of nerve-fibres situated in the superficial layers as the true terminations of the conjunctival nerves. Krause could not see this plexus by reason of his method, which consisted in a maceration of the preparation in vinegar or liquor potassæ, since the first reagent destroyed the superficial layer of the mucous membrane, while the second rendered all the tissues so transparent that the pale fibres could not be recognized. According to Arnold, the terminal corpuscles of Krause owe their existence to a laceration of the double-contoured nerve-fibres, followed by an extravasation of myelin and a rolling up of the torn fibre; this laceration is caused partly by manipulation, and partly by the reagents employed by Krause. The extravasated myelin and the curled up fibre simulate the inner corpuscle; the neurilemma of the torn fibre appears to be the connective-tissue investment of the corpuscle, while the terminal fibre is represented by the surviving axis-cylinder. In every case the peripheric prolongation of the fibre could be found, and so also, though perhaps with some difficulty, extremities and fragments of the nerve sheath, at the periphery of the so-called terminal corpuscle.

* Virchow's *Archiv*, Bd. xxvi.

The objections of Arnold have found opponents in Lüdden and Frey, who regard the existence of the terminal corpuscles as well established.

Helfreich now gives the following details as the result of his own researches:—

The points of entrance of the nerves destined for the conjunctiva are at the inner and outer angles of the eye; from these points the individual twigs branch off from the principal trunks in a more or less curved course. It is, however, the trunk which enters the conjunctiva at the inner commissure, which contains the greatest number of fibres, and which consequently is more voluminous, and gives off by far the greater number of branches. This method of distribution was confirmed in all the preparations which were examined, and minor deviations, such as for instance a more supero-internal entrance of the median trunk, were only occasionally to be observed. By means of a rapid division and ramification of the principal trunks there is formed, especially at the inner angle of the eye, a dense and delicate plexus, which, by an interchange of a few of its smaller fibres, communicates with the plexus of the opposite side. The greater part of the branches forming this plexus pass toward the anterior half of the conjunctival sac, namely, toward its tarsal portion, while the fornix contains only a few small twigs, and not more than a third or a fourth part of the nerve fibres are distributed to the visceral portion of the conjunctiva. As has already been remarked, the number of nerves entering the conjunctiva at the inner commissure is far larger than at the outer commissure, and this preponderance prevails also in the further distribution of the nerves, notwithstanding the large quantity of fibres here given off to the membrana nictitans; for the nerves coming from the inner commissure pass beyond the sagittal or middle line of the conjunctival expansion, so that only the smaller lateral portion of the conjunctival sac is supplied by nerves coming from the outer commissure. In regard now to another relation, namely, that of the under to the upper lid, in respect to the distribution of nerve fibres in each, this differs more or less, according to the special anatomical conditions of the animal in question. For instance, in the Frog, where the membrana nictitans, by reason of its peculiar arrangement and extent, not only takes the place of the under lid, but also performs most of the functions which in other animals fall to the upper lid, the nervous supply of the latter is considerably less abundant than that of the membrana nictitans. A somewhat modified arrangement is found again in Birds, where indeed the nictitating membrane exists as an integral portion of the conjunctival sac, but the under lid exceeds the upper lid in anatomical extent and in physiological importance. In the higher animals, on the contrary, in Mammalia and also in Man, the conditions are the opposite of those in the Frog, and a more abundant nervous supply is given to the upper than to the under lid. According to their origin, the internal or medial nerve-trunk is to be considered as one of the terminal branches of the nervus infra-trochlearis, and the lateral trunk as a branch of the nervus lachrymalis; and these two arise from the first division of the nervus trigeminus.

After forming the coarse plexus in the subconjunctival and deeper layers of the conjunctival tissue, the nerves pass gradually forwards, subdividing as they advance until the remaining twigs contain but a few fibres; the branches which are meanwhile given off never communicate in such a way as to form anything like a plexus. The arrangement of the last nervous subdivisions, which consist still of (2–3) double-contoured fibres, is in some animals, for instance in the Frog, so regular that it is worthy of a more minute description at this place. After these twigs have ascended to a

plane immediately beneath the last layer of the capillary plexus, another subdivision takes place, by which the diverging, still double-contoured fibres generally pass off in a course nearly at right angles to the axis of the twig; in this direction they may be followed for some distance, taking a perfectly straight or slightly wavy course. Thus a system of more or less parallel double-contoured nerve fibres is formed just beneath the capillary plexus. The arrangement and distribution of these ultimate fasciculi of double-contoured fibres is much less regular in other animals, and no further description of them is necessary than to say, that they ascend gradually in an oblique or perpendicular course beyond the blood-vessels to a point, where at the last subdivision the dark fibres are transformed into non-medullated fibres. An exception to this gradually ascending course is made by certain fibres, as was observed by Helfreich in various animals, in a considerable number of perpendicular sections, although not in surface sections. In these cases a single fibre arises from a trunk, consisting of a considerable number of double-contoured fibres, and situated in the midst of the basis-substance of the conjunctiva; this fibre loses at once its medullary sheath, and, passing abruptly upwards, enters at right angles the subepithelial plexus of pale nerve fibres, in which it may be traced for some distance. These appearances may be readily seen in perpendicular sections, which are made a little obliquely.

It is important also to mention those pale fibrils which enter the conjunctival tissue in the same plane with the coarse vascular and nervous trunks, and which are distinguished by their very tortuous course, and by their long continuance in a course once chosen; in consequence of this they pass very slowly forward, and, entering the common subepithelial nervous expansion, are lost to any further separate observation. In their course these fibres often come in contact with the large vascular trunks, and form manifold loops about and around them; they also follow for considerable distances the course of the vessels themselves, and since these relations can only be observed in rather thick sections, it is often impossible to follow them for any great distance. Helfreich nevertheless succeeded in a large number of preparations in following the fibres up toward the epithelium, and in seeing them join the plexus, which is situated just beneath the epithelium. During their extended course these fibres exhibit numerous varicosities and many collections of nuclei.

As already stated, the last subdivisions of nervous twigs are composed of two, or at most three, double-contoured fibres. These lose their medullary sheaths at the point of their final subdivision, probably not while the fibres are still united. At the angle of separation there is generally a deposit of nuclei, and also a slight varicose swelling, from which the pale fibres arise.

The course of these fibres is exceedingly extensive, and a single fibre may often be followed through several fields. Their direction is an essentially straight one, and only occasionally we may remark slight tortuosities or a gradual deviation into a more elevated plane, or a crossing over or interlacing with a capillary loop. The number of these non-medullated fibrils as they ascend through the capillary plexus becomes very great, so that the sum of these intracapillary fibres lying just beneath the epithelium exceeds by many times that of the fibres in the original trunks, as they enter the conjunctiva. Naturally the number of fibrils in isolated portions of the conjunctiva is very various, and at the same time relatively small, so that a direct counting and following of the individual elements up to their terminations may readily be attempted.

Since, therefore, the individual more voluminous fibrils give off branches

throughout their extended course, and these branches in turn repeatedly subdivide, there results a very compact plexus of coarser and finer pale fibres, which gradually makes its way through the layer of capillary vessels, and arrives at a plane immediately beneath the epithelium. The fine fibrils situated directly under the epithelium run for a considerable distance, giving off at acute angles infinitely fine branches, and finally terminate close under the plane of the deepest layer of cells. These appearances may be easily observed in preparations from which the epithelium has been removed, at points here and there where some of the cells have remained. The above description has been taken from such preparations.

Morano,* under the direction of Stricker, occupied himself for several months in researches concerning the terminal nervous apparatus of the conjunctiva, but with very meagre results. The passage of the nerve fibres between the epithelial cells could sometimes be conjectured, but not confirmed with any certainty. Still these researches have rendered it not unlikely that more fortunate microscopists may be successful in following the nerves into the epithelial layer.

The tunica sclerotica † is bounded anteriorly by the tunica cornea, while posteriorly it is separated by a constriction from its prolongation, the fibrous sheath of the optic nerve. At the point where the optic nerve enters the cavity of the sclerotic, the connective tissue surrounding the individual fasciculi of its fibres unites with the tissue of the sclerotic. If we remove the optic-nerve fibres by maceration, this union remains in the form of a thin lamina, perforated by many small holes, and continuous with the inner surface of the sclerotica. This is the so-called lamina cribrosa. Its holes correspond to the individual fasciculi of optic-nerve fibres which pass through it. In the centre we may distinguish two larger holes, situated close together, through which pass the retinal vessels.

The tunica sclerotica increases gradually in density and uniformity from without inwards. In the very compact tissue of its smooth internal surface are deposited, especially in dark-eyed individuals, a certain number of irregularly formed, flat pigment cells, with knob-like or radiating processes: when these are present in great quantity they give a brownish color to the surface.

The arrangement of the fibres of the sclerotic was first described by Valentine.‡ His statements were confirmed by Brücke only so far as that, in general, fibres could be found in the sclerotica running from behind forwards, and also circular fibres; these fibres interlace with one another, forming a dense mat-work; also the fibres of the tendons of the recti muscles after they have reached the sclerotic spread out in fan-shaped expansions, and, uniting with the mat-work of the sclerotic, materially strengthen its anterior portion.

The connective-tissue nature of the fibres of the sclerotic has been already discussed in this text-book (see page 73). Cellular elements, similar to the corneal corpuscles, are embedded in the basis substance. If we touch the sclerotic of a living Rabbit with the stick of nitrate of silver, we may see in surface sections, after complete reduction of the silver, the delicate markings of the serous canals. On the other hand, the preparations treated with the chloride of gold furnish the positive to the negative pictures of the silver preparations. The latter appearances I have indeed seen but once, in a preparation shown me by Dr. Carmalt, of New York; but in this case they

* *Centralblatt.* April, 1871.

† Brücke, *Anat. Beschreibung des menschl. Augapfels.* Berlin, 1847.

‡ Repertorium, Bd. i. Heft iv., p. 301.

were so sharply delineated that there could be no doubt as to their existence. The cells lying in these spaces contain pigment granules in many of the Mammalia.*

In Birds the sclerotica consists of hyaline cartilage, which is covered externally and internally by connective tissue. At the anterior margin of the sclerotica, and sometimes also around the entrance of the optic nerve, the Birds have a bony ring made up of separate bony scales.

Also in Amphibia and Fishes hyaline cartilage is present in the sclerotica. Helfreich † in his treatise on the nerves of the sclerotica has also given some details concerning the structure of the Frog's sclerotica, which are as follows:

Closely attached to the external surface of the layer of faintly rose-colored cartilage, containing exceedingly clear and beautifully marked cells, lies the layer of connective tissue; this layer is of a rather dark green color, and is composed of very compact parallel and perpendicular bundles of fibres; external to it, and separated by well-defined limits, is the surrounding investment of loose connective tissue. Both the layer of connective tissue and of cartilage were seen, in sections running the whole length of the preparation, to be of different thickness at different points. The layer of cartilage is thickest at the posterior pole of the eyeball, growing rapidly thinner as it passes forward, and terminating with a rounded margin at a point just before reaching the insertion of the recti muscles: the layer of connective tissue has an exactly opposite arrangement with regard to its thickness at different points. The layer of cartilage is homogeneous in texture throughout, presenting nowhere interruptions or intervals for the passage of vessels and nerves; on the other hand, in the stratum of connective tissue these exhibited themselves with the same beauty and elegance as in the surface sections. In the posterior portions of the longitudinal sections the coarser trunks and double-contoured fibres could be seen; and more anteriorly, as far forward as the termination of the cartilage-layer, and farther, the fine, light violet-colored axis cylinders might be followed for some distance in their straight or slightly tortuous course. In some places these latter displayed slight varicose swellings; in regard to their course it was to be remarked, that they gradually tended toward the boundary-line between the cartilage and the connective tissue.

The larger nerve trunks, everywhere consisting of rather loosely united double-contoured fibres, after repeated division as they pass gradually forward, exhibit throughout a very distinct continuity with the long axis cylinders already mentioned. The transition from one to the other takes place in such a way that a trunk consisting of two double-contoured fibres loses its medulla at the point of separation of its fibres. This sudden breaking off of the medullary sheath can everywhere be satisfactorily seen by varying the focal adjustment, as well as the gradual course of the pale fibrils toward the boundary-line between the layer of connective tissue and the cartilage. By continued subdivision the axis cylinders undergo a rapid increase in numbers, exactly in the same way as was described of the subepithelial plexus of the conjunctiva. These fibres become finer and finer, and after an extended course finally terminate, as fibrils of exceedingly small diameter, in the substance of the fibrous membrane, not far from the layer of cartilage. In their course they interweave abundantly, but never blend together in such a manner as to form a true plexus. Their extremities are distinguished by no increase in diameter, but rather by a decrease in it, since they simply taper off to a point. During their entire course they are seen to be

* Leydig, l. c.

† L. c.

very often in contact with the numerous connective-tissue corpuscles of the fibre-bundles, although, notwithstanding the most careful examination, their extremities were never found actually to communicate with the processes of the cells.

In the Dove and the Chicken no trace of nerves could be found which might be considered as analogous to the nervous distribution described in the Frog. Throughout the entire circumference of the sclerotica nerve-trunks passing forwards were to be found only beginning at the insertion of the recti muscles; and these, owing to their lack of subdivision, as well as owing to their entire relations, must be considered simply as passing trunks on their way to the ciliary muscle, the iris, cornea, etc. The same results were obtained in the sclerotic of the Mouse and the Rat, in which animals the proper preparation of specimens was very much hindered by the very intimate connection existing between the sclera and the choroid. Nevertheless, here also the anterior expansion of the ciliary nerves was clearly demonstrable. In researches on the sclerotic of the Rabbit a young albino was always selected, and here also the relations of the nerves entering the sclerotic corresponded perfectly with those of the Frog's sclerotic, namely, a primary nervous expansion of the same kind, and a simple division of the trunks, which then abruptly terminated. The entire picture of this distribution was however so typical, and so conformable with the conditions above described in the Frog, that no room for doubt was left that these were the proper nerves of the sclerotica. So also there was no doubt that in this animal the conjunctival nerves terminated just beneath the epithelium, although they were stained by the chloride of gold only as far as the larger axis cylinders.

IX. THE LACHRYMAL GLAND.

By FRANZ BOLL.

1. *General Plan of Structure.*—Agreeing in all essential points of structure with the salivary glands (see chapter xiv.), the lachrymal glands of Man and the Mammalia represent glands of the so-called acinous formation. Like the salivary gland, the lachrymal gland is resolved into a mass of polyhedral bodies of most varied shape, although generally of pretty constant size, by means of a highly developed system of septa arising from the capsule of the organ; these septa penetrate the gland, intersecting each other frequently, and are seen by the microscope to consist of a loose, fibrillar connective tissue. The principal portion of these polyhedral bodies, which we shall designate as the true parenchyma of the gland in a strict sense, is seen in sections to consist almost entirely of alveoli and blood-vessels. In sections of the parenchyma we meet only occasionally with an excretory duct and its accompanying blood-vessels and nerves. The trunks of all these latter structures entering at the hilus of the gland run constantly together, embedded in the loose connective tissue of the septa, whence they enter the parenchymal bodies generally at a right angle, being accompanied only for a short distance by a few fibrils of connective tissue. With the exception of

these scanty vestiges, the so-called interstitial or fibrillar connective tissue is not present in the bodies of the parenchyma.

2. *The Alveoli.*—The forms and dimensions of these structures, which compose the true secreting parenchyma of the gland, are subject to variations within narrow limits. They are sacs in which we differentiate the contents, the secreting epithelium, and the investing membrane (membrana propria). The former are of very various forms: polyhedral structures about equal in size, bordered by a varying number of surfaces, which join each other at very different angles, although almost always with sharp edges.

Upon the surfaces also it is not uncommon to find rather sharp, fine furrows. None of the different diameters of the epithelial cells are developed at the expense of the others, so that they are always of an irregular cubic form. The spherical, homogeneous nucleus, with its not always distinct nucleolus, always occupies an eccentric position, namely, at the base of the epithelial cell near the membrana propria. At this point, as it seems, a rather long and large process, brilliant and taking an intense color from carmine (Heidenhain), passes off from the cell; it terminates however at some distance from the cell without forming any further connections. Its length may be nearly equal to that of the cell itself. Also the other angles of the cell are not unfrequently lengthened out to form processes, whose length, however, is generally considerably under that of the basal process. The nucleus also often exhibits a pointed process, which however can never be followed beyond the limits of the cell itself, and which is always situated in the direction of, or even within, the basal process.

As was first shown by Henle and afterwards pointed out by Heidenhain, the acinous glands are divided into those whose secretion contains mucus, and those in which it is wanting. These characteristics of the secretion are accounted for by the histological nature of the secreting parenchyma, and more especially of the glandular epithelium, which in the latter always remain protoplasmic, while in the former the protoplasma of the cell undergoes a metamorphosis into mucus, which is very easily seen with the microscope. The lachrymal gland of Man and of the animals examined (Sheep, Ox, Horse) belong to the latter class. Not a single cell which has undergone a mucous degeneration is ever to be found in its parenchyma. We may therefore conclude with certainty that the secretion of the lachrymal gland never contains mucin.*

According to the researches of Heidenhain, the so-called lunula, first described by Giannuzzi, presents in sections a generally crescent-shaped collection of protoplasmic cells, which are perhaps destined to replace the glandular cells which have been destroyed by the mucous metamorphosis. It is plain that, since the lunula belongs only to those glands where a mucous degeneration of the secretory elements takes place, we cannot expect to find a lunula in the lachrymal gland, whose cells, like the epithelium of the submaxillary gland of the Rabbit, always retain their protoplasmic character.

The alveoli are invested by a fine membrane, the so-called membrana propria. The structure of this membrane is very characteristic. It is everywhere composed of several flat, stellate cells, which are in manifold

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* The only analysis of the Human tears found in literature (Frerichs' "Thränensecretion" in Wagner's *Handwörterbuch der Physiologie*, iii., 1, p. 618) gives, it is true, a small quantity of mucus. But here the secretion of the Meibomian glands was not excluded.

communication with one another by means of their often very abundantly developed processes, which pass around the alveolus like hoops. These finely striated processes, proceeding from the nucleated centre of the cells, sometimes narrower and sometimes wider, always however lying flat upon the curved surface of the alveolus, do not represent a wicker-like, interrupted investment of the alveolus, but rather a system of thickened stripes and ribs in a membrane completely and closely surrounding the alveolus, and formed by the stellate cells in a way which it is doubtless not easy to describe. The cells with their processes, in their relations to the substance of the membrana propria, may be best compared to the ribs of a leaf, or to toes between which a web is stretched. A perfectly sharp dividing line between the ribs and the substance of the membrane, from which one might conclude that the stellate cells were separate structures from the membrane, does not, however, exist. There exists here a real histological unity; the thicker longitudinally striated ribs are not to be separated from the basis substance of the membrane, but are gradually and insensibly continuous with it. And the membrane itself generally exhibits a gradually fading longitudinal striation on either side of the ribs and running parallel to them.

This description of the structure of the membrana propria (of the correctness of which one may easily convince himself, especially in teased preparations from glands treated with iodized serum, or at the free edges of agitated sections from glands carefully hardened in Müller's fluid) gives the most satisfactory reconciliation of the diverse appearances often presented in the same preparation, owing to a greater or less degree of maceration and a more or less easy dissolution of the tissue. Thus we may obtain from glands macerated in iodized serum or diluted Müller's fluid, by tearing up the specimen with needles, appearances which appear diametrically opposite and entirely unreconcilable. Sometimes we find isolated alveoli whose epithelium seems to be shut up in a sac, closed on all sides, and generally with rather firmly knit homogeneous walls; sometimes groups of bare epithelial cells, which still preserve the form of the alveoli, and to which are attached a few isolated stellate cells. Again we may see floating in the fluid the forms of the wicker-like frames of the alveoli, composed simply of the stellate cells with their processes, and in the hollow of which are generally still to be found a few secretory epithelial cells. In company with a numberless quantity of isolated glandular cells are also to be found the isolated cells of the membrana propria. The form and number of these are subject to considerable variation. In young animals (best seen in the Calf) they are larger, the central portion as well as the processes being more strongly developed. The centre of the cell is protuberant, and at the same time bulged out almost like a vesicle, so that the cell seen in profile often presents the appearance of a crescent, which in sections of hardened glands not infrequently surrounds an alveolus. If the fluid under the glass cover be agitated, we may often observe under the microscope the transition of such a crescent into a stellate multipolar cell. In young animals a small quantity of granular substance lies in the centre of the cell surrounding the usually round nucleus, which does not contain a distinct nucleolus. In older animals even this small vestige of protoplasma is almost entirely wanting. The substance of the flat, often almost band-like, processes is pale and at the same time finely striated. The division of the processes takes place dichotomously at a more or less acute angle; not infrequently also a large process may be seen to divide at once into several branches.

A portion of the processes of these stellate cells penetrate, as may also be

seen in specimens prepared with a view to isolation, even between the epithelial cells of the alveolus. Pflüger, who first paid special attention to these cells in the salivary glands, affirms that a real continuity exists between their processes and the processes of the secretory epithelium; that both cell-forms communicate with one another by their processes, upon which communication with true epithelial structures is founded the idea of the nervous nature of the stellate cells. Although I have often seen appearances which at the first glance seemed to indicate a material continuity between these two forms of cells, still I have not yet been able satisfactorily to convince myself that any communication in reality existed.

3. *Interstices of the Alveoli.*—While the internal surface of the membrana propria is lined by the epithelial cells of the alveolus, the external surface remains free, and serves as the boundary of a space filled during life with lymph; this space in each parenchymal body of the gland lies everywhere between the external wall of the capillaries and that of the alveolus, and may be demonstrated by the most varied methods (injection by puncture, artificial œdema of the gland) (Ludwig).

The form and the boundaries of this hollow space in the secretory parenchyma of the gland must naturally be enormously complicated. In sections of isolated, injected parenchymal bodies (best with cold solutions of Berlin blue) each separate alveolus appears universally and regularly surrounded by a colored ring. The uncolored alveoli lie each in a colored ground, a picture which is often maintained with complete regularity over a surface of 40–50 alveoli. If at the same time the blood-vessels have been colored differently, for instance, with red, the irregular, characteristically inconstant distribution of the vessels colored with red forms a very remarkable contrast with the universally regular arrangement of the system of canals injected with blue. In a thin section the blood-vessels, whether seen longitudinally and as red tortuous lines, or whether cut transversely and appearing simply as red points, are always surrounded by a blue-colored space, the same space which also surrounds each alveolus. These appearances, repeated as they are with perfect regularity in every section, can have no other interpretation than that an exceedingly rich, uniform, and connected system of fissures ramifying throughout the entire gland surrounds all the alveoli and blood-vessels. These are not single sheaths surrounding the alveoli and blood-vessels, not separate perialveolar or perivascular spaces, but for each parenchymal body a universal and very complicated space, separating the blood-vessels from the alveoli at every point, and which must be traversed by everything which the blood brings to the secretory parenchyma before it can be transformed into secretion.

The already intricate histological and topographical relations of this space is still more complicated by the fact that a very abundant system of broader and narrower fibres, as if from stellate cells between the alveoli, is spread out in the space lying within the secretory parenchyma. This system of cells with their processes, lying between the alveoli, may be very easily demonstrated in sections of hardened glands. It stands in part in immediate connection with the stellate cells forming the membrana propria, some of the processes of which pass over to the adjacent alveoli, so that the walls are more or less intimately joined together. Not infrequently may be found cells, situated between two alveoli, which belong as much to the investing membrane of the one as to that of the other, and send processes to both. Also quite free cells are often to be found attached only very loosely between the alveoli by means of their processes. It is noticeable that these interstitial connective-tissue cells are connected only with the

external wall of the alveoli, but never with the capillaries, which are entirely destitute of an adventitia capillaris.

Giannuzzi, the discoverer of this system of fissures traversing the secretory parenchyma, considers them as true lymph-spaces, that is, in communication with genuine lymphatic vessels, and capable of being injected from these; being analogous to the spaces described by Ludwig and Tomsa as surrounding the canaliculi and blood-vessels of the testicle, which were in fact injected through the lymphatic vessel of the spermatic cord. This demonstration, it is true, has not as yet succeeded with the spaces of the parenchyma of the acinous glands. Numerous attempts have failed, owing to the delicacy of the lymphatic vessels of the gland, and owing to the obstructions presented by the valves. It is not uncommon to find, in preparations injected by the method of simple puncture, appearances which make it at least very probable that these spaces in the parenchymal bodies are in direct communication with real, circular lymphatic vessels running in the fissures which separate the individual parenchymal bodies. As yet, however, the relations of the spaces within the individual parenchymal bodies (here histologically sharply limited by the external surface of the membrana propria and the capillary blood-vessels) to the coarser trunks of the excretory ducts and the blood-vessels, as well as to the connective-tissue septa, are not sufficiently well defined.

4. *The Excretory Ducts.*—The lachrymal ducts are lined by a single layer of low, cylindrical epithelium. In the interior of the gland the ducts divide up quickly into numerous branches, which are likewise lined by low, cylindrical epithelium, and from which arise those passages which Pflüger called, in the salivary glands, salivary tubes, and which may be best designated as the lachrymal tubes. Their lumen is generally narrow; they are lined by a characteristic tall cylindrical epithelium, whose basal end always displays a distinct fibrillation, which was most thoroughly examined by Pflüger, and said to have some relation to the regeneration of the glandular tissue. From these canals, lined with tall cylindrical epithelium, abundantly fibrillated at their basal ends, and which seem to exist in all similarly constructed acinous glands, are at last given off, either by gradual transition or more abruptly, rather long fine tubes not much larger than capillaries. The characteristic peculiarity of these tubes, the same in all similar acinous glands, consists in the fineness and dimensions of the cells forming these simple epithelial tubes. These are always very flat, and generally distinguished by the possession of quite voluminous processes, which give to the cell a somewhat fusiform appearance. They lie with their long axes parallel to the axis of the epithelial tube, and often by means of their processes assume an imbricated arrangement. These tubes finally connect with the alveoli through short branches, which are formed generally by 4–6 epithelial cells, and are continued into the interior of the alveolus, where they are almost completely surrounded by the true secretory epithelium. These cells of the excretory ducts, situated almost in the centre of the alveolus, and penetrating with their processes between the secretory epithelial cells, are designated in the pancreas by Langerhans as central acinal cells.

While formerly the cavity within the alveolus, into which the secretory epithelium empties its secretion, was described as very simple in form, researches more recent and aided by better methods of injection (Giannuzzi, Langerhans, Ewald, Saviotti) show that the simple short and fine excretory duct of the alveolus is resolved into a very rich, abundantly branched and anastomosing plexus of minute circular canaliculi, which surround and

enclose in their meshes the individual epithelial cells—exactly as Hering has described the relation of the finest gall-ducts to the liver cells. The canaliculi are destitute of a special membrane, and are nothing more than passages left between the adjacent polyhedral glandular cells, which are of various form, and whose edges as well as surfaces are provided with furrows.

5. *The Nerves.*—The nerves of the lachrymal gland always follow the same course with the branches of the blood-vessels and excretory ducts. They are for the most part non-medullated, even in the main trunk of the nervus lachrymalis. I have never been able to follow them with certainty over the lachrymal tubes, which they always accompany, and can state nothing definite with regard to their final terminations, or their anatomical relations to the secretory elements. At all events, no nerves are to be found within the parenchymal bodies in the interstices between the alveoli, and if they in reality enter into direct relations with the secretory epithelium, they must pass to the alveoli with the finest excretory ducts.*

6. *The Literature.*—The histological literature of the lachrymal gland coincides for the most part with that of the acinous glands. Passing over the older authors, I give the complete literature since the researches of Giannuzzi, which proceeded from the laboratory of Ludwig and formed an era in this branch of study; also the almost simultaneous and not less important works of Pflüger.

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* Appearances, such as I drew in my first work, where non-medullated nerves pass upon the blunt end of the alveolus, can only be exhibited at the edge of the parenchymal body toward the septa of connective tissue.

CHAPTER XXXVI.

THE ORGAN OF HEARING.

I. The External and Middle Ear exclusive of the Eustachian Tube.

By J. KESSEL.

In the organ of hearing of the higher Vertebrates we distinguish a sound-conducting and a sound-perceiving apparatus. The conducting apparatus includes the external and middle ear, while the percipient elements are contained within the inner ear, in the vestibule, the semicircular canals, and the cochlea.

A. The External Ear

includes the auricle, the external meatus, and the membrana tympani.

The auricle, with the exception of the lobule, is chiefly composed of a cartilaginous plate of complicated form which gives it its well-known shape. The cartilage belongs to the reticular variety, is 1–2 mm. thick, and covered by a perichondrium rich in elastic fibres. These fibres pass into the substance of the cartilage, forming fine anastomoses with each other (Rollett, page 90 of this manual); and in the meshes of this network small cartilage cells are embedded.

Of the muscles which are attached to the auricle only those are spoken of here which pass between its different regions. They are small, thin, striated muscles, and are inserted with short tendons on the perichondrium.

The cutis of the auricle, a continuation of that of the face and skull, covers the cartilage, and by a duplicature forms the lobule. Over the whole surface downy hairs are found, into the sheaths of which sebaceous glands from 0.5–2.0 mm. in diameter enter. These latter reach their greatest size in the concha, where they are larger than the fine hairs, so that their openings can be seen with the naked eye as small depressions. In some individuals, however, at the entrance of the external meatus the opposite is the case, and the hairs reach such a development that they have been named by anatomists bucks' hairs. Small sweat glands of 0.15 mm. diameter are found on the surface of the auricle, chiefly on the side next the skull.

The subcutaneous tissue of the external skin of the auricle is not the same throughout. Numerous elastic fibres are woven into its substance, and these can be followed through the perichondrium into the reticular cartilage. This tissue, on the concave surface, forms a thin layer which is firmly united with the perichondrium, and on this account the skin on this spot is immovable. On the convex side of the auricle, however, the subcutaneous tissue increases in thickness and the skin is there movable: at the lower portions of the auricle it contains in its meshes fat-cells, which chiefly give the form and thickness to the lobule.

The auricle receives its blood from different sources. The capillaries coming from the arterial branches are distributed in the cutis, in the hair bulbs and glands, and also in the cartilage. Some of the vessels pass di-

rectly through the cartilage from the inner to the outer side (Pareidt, 31), while others remain in the perichondrium. Branches from these latter pass into the substance of the cartilage and are there distributed (Meyer, 28). Nerves are most abundant on the convex surface of the auricle, less abundant on its concave surface and on the lobule. The coarser nerve-branches run along the larger vessels, and pass through the medial side of the cartilage in order to reach the skin of the lateral surface.

The *external meatus* consists of a cartilaginous and an osseous portion which together are 24 mm. long (Tröltsch, 45), the former 8 mm. and the latter 16 mm.; the width of the meatus depends upon individual peculiarities. The cartilaginous portion is a part of the cartilage of the auricle and of the tragus; it forms a groove open on its posterior and upper part, which is converted into a tube by fibrous tissue. It is joined to the osseous meatus by a small band of connective tissue in such a way as to be movable. This cartilage is of the same structure as that of the auricle, and in order that it may be more movable upwards and backwards, has two slits on its anterior and lower wall, which are closed by fibrous tissue. The cutis of the external meatus is a continuation of the outer skin of the auricle and tragus. It is not of the same consistency throughout, but varies in thickness and minute formation. That of the cartilaginous meatus is $1\frac{1}{2}$ mm. thick, contains downy hairs with their sebaceous glands, ceruminous glands, and a little fat in its subcutaneous tissue; in the osseous portion of the meatus it changes its character; its thickness diminishes to 0.1 mm., the downy hairs become extremely fine and few in number, and the ceruminous glands are found only on the posterior upper wall, where they are generally seen even to the membrana tympani. Small papillæ arranged in long rows are found under the cuticle, and also a corium, with abundant elastic fibres, which, in their lower layers, pass into the periosteum. The ceruminous glands resemble the sweat glands, not only in the time and manner of their development, but also in their external form and their minute histology; this is also true of the contents of the ceruminous glands, so far as the microscope allows us to judge, the only difference being that in cerumen masses of very fine corpuscles of coloring matter are found (*vide* p. 553). The ceruminous and sebaceous glands together secrete a yellowish-white, rather fluid substance, which consists essentially of small and large fat globules, masses of corpuscles of coloring matter, and cells in which single globules of fat and coloring matter are embedded; in addition to these, hairs and scales of epidermis from the lining of the meatus, and foreign bodies of different kinds are also found. Where the cerumen has collected in considerable quantity and remained some time in the external passage it alters its color, and forms, from the loss of its watery contents, solid masses.

The larger arterial branches run along the upper and posterior wall of the meatus, and give off a large branch which passes on to the membrana tympani. The principal nerves which are found in the cutis of the cartilaginous meatus divide into numerous branches in the osseous portion, so that, in the deepest parts of the passage, the surface supplied with nerves is much greater than in the external portions, thereby giving the great sensibility to this part.

The membrana tympani stretches across as a dividing wall between the external meatus and the tympanum.

Its form is in general elliptical, but the regularity of the ellipse is broken in it upper and anterior portions by the segment of Rivini. The long axis of this ellipsoic passes forwards and downwards, the shorter backwards and downwards; the diameters of the membrane should therefore be measured in the direction of the axes

of the ellipsoid, and not vertically and horizontally, as is usual. In the former case the measurements are 9.5–10 mm. for the long axis of the ellipsoid, and 8 mm. for the shorter; in the latter the horizontal diameter is 8–8.5 and the vertical 8.5–9 mm.

The planes which would pass through the grooves in which the two membranæ tympanorum are inserted, are so inclined to each other as to form an obtuse angle upwards and an obtuse angle backwards, the former of which measures 130°–135°, the latter, however, has not yet been determined. The membrana tympani itself does not lie in the plane of the groove in which it is inserted, but the surface is so curved that the membrane resembles a funnel, the point of which lies at the end of the manubrium of the hammer; the meridian lines of this funnel, moreover, instead of being straight, are convex on their external surface.

For examining the position of the different elements constituting the membrana tympani, an intact membrane, seen with a slight magnifying power, is the most useful. For this purpose the membrane with its osseous border and with the ossicula should be dissected from the petrous bone and laid for some hours in water, so that the greater part of the epidermis which obstructs the view may be removed. The preparation is then to be deprived of its water by lying in absolute alcohol, rendered transparent in oil of turpentine and allowed to dry. With slight magnifying power three layers can now be seen, an external, a middle, and an internal; these are attached throughout their whole periphery except at the segment of Rivini by means of a thick edge to the fibrous ring which is inserted in a groove of the bone. The external layer is a continuation of the cutis of the meatus and resembles this in all important particulars. The middle layer, the thickest of the membrana tympani, consists of broad fibres with sharp outlines, the majority of which run to the hammer in a radial or circular direction; a small number, however, run in different directions between these circular and radial fibres. The radial layer lies external beneath the cutis, the circular internal beneath the mucous membrane.

The inner or mucous layer of the membrana tympani is a direct continuation of the mucous membrane of the tympanum; it is very thin, and on account of its complicated structure can only be examined with strong magnifying powers. Although it is easy to convince one's self of the general arrangement of the elements constituting the membrana tympani, the minute structure of the segment of Rivini is not so easily determined, as the views of authors in regard to it differ widely. The osseous groove in which the membrana tympani is inserted does not run round completely into itself, but in its upper part a section of the bone in the form of an oval segment is wanting, and the two ends of the tympanic groove could only be united by a cord of this segment 2.5–3 mm. long; this space is known as the segment of Rivini. This Rivinian segment is filled by the tissue of the cutis and the mucous membrane of the tympanum. The tendinous ring of the membrana tympani bends with the greater part of its fibres from the direction which it has hitherto maintained, and turns at this point towards the deeper lying processus brevis where it is inserted, while the remainder of the tendinous fibres of the ring pass upwards and are lost in the connective tissue of the periosteum. In this way an irregular triangular space is formed, bounded above by the Rivinian segment, and on each side by two bands which attach the hammer, or rather the point of its small process, to the anterior and posterior corners of the osseous groove. The anterior band is 1.5, the posterior 2 mm. long. The three points of insertion of these bands do not lie in a perpendicular plane, but the two lower ones arise just so far external to the upper one as the short process of the hammer has pressed the membrana tympani towards the meatus, so that a perpendicular line from the Rivinian segment downwards would pass through the neck of the hammer.

The distance from the highest point of the segment to the point of the short process is 2.5–3 mm.

The tissue filling the above-described space, called by Odo Schrapnell (40) the membrana flaccida, is less firmly stretched than the rest of the membrana tympani, and sometimes even falls inwards, pouch-like, towards the tympanum (Henle, 12). It consists of a very thin layer of cutis and of the mucous membrane of the membrana tympani. The cutis contains, in addition to the vessels and nerves, undulating bands of connective tissue, which pass obliquely from the posterior and upper part of the meatus and become the circular fibres of the anterior superior segment. The thin stratum of mucous membrane reaches to the osseous edge of the Rivinian segment, and from here passes over to the projecting neck of the hammer, which lies opposite.

The supposition that a Rivinian perforation exists under normal circumstances has been thoroughly disproved by Hyrtl (16) and other observers; it is found only as the result of inflammation. I have convinced myself of the correctness of this view in dissections, and lately, at Dr. Gruber's, directly on living persons.

After this general view of the topographical relations of the membrana tympani, I pass to a description of its minute microscopic structure.

The cutis of the osseous meatus passes from all points of its circumference directly on to the membrana tympani, but the hairs and glands which are found in it are wanting entirely on that membrane; the papillæ only extend to the tendinous ring except in the posterior and upper part, where they are found as far as the processus brevis, and the rete Malpighii shows on other portions of the membrana tympani a generally smooth, but here and there an undulatory surface. On a fresh membrana tympani, treated with perosmic acid, the epithelium is colored black exactly as far as the layer of epidermal cells, just as in the meatus.

The epidermal cells, the cuticle, and the corium diminish gradually in thickness from the periphery towards the handle of the hammer, then increase again, and reach the greatest thickness on the outer edge of this bone. The reason of this is, that the vessels and nerves of the cutis and the membrana propria, which are accompanied by strong bands of connective tissue, pass obliquely from the posterior and upper wall of the meatus toward the handle of the hammer and then along and over it. A part of the connective-tissue bands surround the end of the hammer, and unite on the anterior side with those bands which accompany the ascending veins of the hammer-plexus.

Aside from the above-described general relations of the cutis of the membrana tympani, the thickness of the cuticle is subject to many individual variations. It is well known that the cells of the cuticle after death become rapidly opaque and are easily separated, so that frequently it is impossible to decide from sections whether we have all the layers before us, or whether the most superficial of them have been separated. We must of course take into consideration these pathological changes, which are frequently found, in order to escape error in deciding the normal thickness.

I have considered these sources of error, and from numerous measurements have come to the conclusion that the thickness of the cuticle varies very much in Adults. How far the thickness of the cuticle of the membrana tympani influences its sensibility and the performance of its regular physiological functions cannot as yet be determined with certainty. From the external skin it might be supposed by analogy that here also a slight development favors greater sensibility. The thickness of the cuticle of the membrana tympani in new-born Children also favors this view.

The membrana tympani consists of sharply outlined, opaque fibres, flattened on the sides, swelling out in the middle, and from 0.0036–0.0108 mm.

in thickness. They appear under certain conditions homogeneous, but are in fact fibrillated. The fibrillated structure of the fibres appears distinctly on the addition of reagents, such as chromic acid, chloride of gold, osmic acid, etc. The fibres of the membrana tympani resemble most nearly the fibres of tendons and have the same chemical characteristics; they swell in solutions of potassa and acetic acid, and the fibrillæ separate in lime and baryta water, owing to the solution of their connecting substance. If the membrana tympani is boiled in a weak solution of potassa it is dissolved, and only a slight remnant of elastic tissue is left behind, which shows distinctly in some parts the tubes of vessels, in others a very thin continuous membrane, which apparently forms the foundation of the mucous layer on the inner side of the membrana tympani (Helmholtz, 11). The embryonic membrane is very well adapted to examining these fibrillary bands. The membrana propria is here represented by distinct bundles of fibrillæ in all stages of development. No boundary exists in the earlier periods of development between the connective tissue of the cuticle and the fibres representing the membrana propria; this distinction can first be made out toward the end of fœtal life.

The membrana propria might therefore be described "as a deep layer of the corium changed and adapted for physiological purposes." On a well-teased preparation of an adult membrana tympani we can see how the glistening bands divide up and pass into the thin layer of fibrillary tissue in the cutis, and also into the deeper tissue of the mucous membrane. From the close union of the fibrillæ with their connecting substance, and their union with each other to form strong broad bands, they become very resistant to tension, and form an almost inelastic membrane, a condition due to the method of their union, which is to be more minutely described, and which is of the greatest importance for the conduction of sound, as Helmholtz (11) shows. These fibres run in the special layers already described, either parallel or crossing each other at very sharp angles, and frequently unite together, leaving slits and large spaces between.

These spaces are usually empty and then appear glistening, or else on their edges they are covered with a finely granular mass. Sometimes in addition to the nerve fibres, to be hereafter described, cells are found which exactly fill them. These cells, called by v. Troeltsch (44) the corpuscles of the membrana tympani, appear sometimes spindle-shaped, sometimes star-shaped, according to their position in the field; in the former case they are seen in profile, in the latter, *en face*.

The larger spaces are provided with encapsuled nuclei and are frequently filled with amœboid cells. By the aid of injections, and coloring with chloride of gold, it becomes evident that we have to deal here with vessels passing transversely and obliquely.

On the periphery the thin layers of the membrana tympani interweave, leaving large and small spaces between the fibres for the passage of vessels, and form from their union with the tissue of the cutis of the external meatus and that of the tympanic mucous membrane a thick swelling, "the tendinous ring," which is attached by means of a thin periosteum to the annulus tympanicus. Vessels and spindle-shaped, nucleated elements are found between the glistening bundles of fibrillæ, and frequently also small cartilage cells, lying singly or in rows. From this it is clear that all the layers of the membrana propria are united to the tendinous ring, and I can confirm Gruber's recent observation, that the circular fibres may be followed distinctly into the tendinous ring, but must also add that these fibres singly, and at some distance from each other, pass off again from the ring

at very acute angles, collect together, and reach nearly as great a thickness as that which results from the union of the fibres coming from the epidermis, cutis, and mucous membrane: on account of the tension of these fibres, the radii of the surface of the membrana tympani are convex towards the meatus. Toward the middle of the membrana tympani the circular fibres increase in number, but are wanting on the lower third of the handle of the hammer and its neighborhood. The layer of circular fibres is particularly well marked on the periphery of the anterior superior segment, because here the fibres which come in an oblique direction from the posterior upper wall of the meatus, and which cross the triangle below the Rivinian segment, are added to those from the tendinous ring.

The variable thickness of the circular layer and of the cutis, which latter, as has been said, is greatest on the periphery and along the handle of the hammer, renders it impossible to decide by any single measurement on the thickness of the membrana tympani; on the periphery and along the manubrium it is about 0.1 mm., but on the parts lying between these two points, where the cutis diminishes in thickness and the circular fibres are thinner or entirely wanting, it is only one-half as much, or even less. The membrana propria is attached to the handle of the hammer, but widely different views have been expressed in regard to the manner in which this takes place. According to v. Troeltsch (45), the manubrium of the hammer is inserted between the two fibrous layers (radial and circular), the former being attached to it while the latter lies behind it, with the exception of some of the upper circular fibres which pass outwards and run external to the hammer. Gruber investigated anew the mode in which the hammer is attached to the membrana tympani, and described a cartilaginous formation, till then unknown, which begins over the short process of the hammer and reaches $\frac{1}{2}$ mm. below the end of the manubrium; on its lower two-thirds this cartilage was firmly united with the manubrium, but above, at the short process, it was not attached, but formed a sort of joint, the cavity of which was filled with synovial fluid. Later investigations by Prussak (36), Moos (29), and myself (17) confirm this thus far, that a third of the short process consists of cartilage, but this cartilaginous passes over into the osseous portion without any interruption. According to Prussak and Moos, a thin layer of cartilage cells is found also under the periosteum of the manubrium, not only in Infants, but also in Adults and aged persons.

I have lately repeated, on preparations from all ages, my investigations on the relations of the structures of the membrana tympani which are connected with the hammer. In embryos of from 3–9 months the ossicles are still in a cartilaginous condition, and hence offer the advantage of cross-sections without further preparation, while in Infants and Adults the calcification must first be got rid of. By preparing such sections as will pass at the same time through the membrana tympani and hammer, it will be found that the latter is surrounded by an independent periosteum distinct from the elements of the membrana propria, and only united with that membrane, or rather the mucous layer of the membrana tympani, by a duplicature of the mucous membrane 0.2–0.3 mm. broad. At the point where the short process is subsequently developed a quantity of brightly glistening nucleated cells are found, under the periosteum and in the tissue of the duplicature. These elements remain through life as cartilage cells, and form a solid mass with the osseous portion of the small process, which is developed toward the end of fœtal life by ossification of the periosteum at their point of union.

At birth a close union of the hammer with the membrana tympani exists only at two points: at the short process where the bands coming down from

the corners of the Rivinian segment are inserted, and at the lower third of the manubrium, where one portion of the radial fibres strengthen the periosteum, and another portion cross in front of the manubrium in order to pass into the irregular layer lying between the radial and circular fibres. The membrana propria is united with the periosteum of the upper portion of the manubrium only by a loose connective tissue, so that a slight mobility of the bone is possible at this point without the existence of any articulation. The attachment of the mucous membrane of the membrana tympani to the hammer is of only slight importance.

The assertion that the tympanum is completely filled up by a young connective tissue during the *whole* intra-uterine life requires limitation, as I have repeatedly found the cavity filled with fluid, and its mucous membrane covered with epithelium, both in the fœtus and Infants.

The mucous membrane of the membrana tympani consists of an epithelium and a fibrous framework below it. The epithelium, which has been heretofore described as a simple layer of pavement cells, has by no means this character in every part, but possesses peculiarities of form such as have been described by Ludwig and Schweigger-Seidel (*Arbeiten aus d. physiolog. Anstalt zu Leipzig*, 1866), on the epithelium of the abdominal surface of the Rabbit's peritonæum. By treatment with silver, polygonal surfaces of variable size and enclosed by meandering lines are brought out on the surface of the mucous membrane.

Fig. 367.

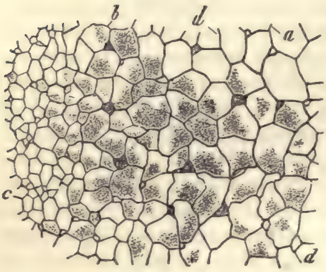

Fig. 367. Mucous epithelium of the Human membrana tympani. Silver preparation.

Where their edges meet, round or triangular spots are seen, which have the appearance of openings, and the probability that they are really such is strengthened from their homogeneous appearance under treatment with iodized serum. Large, small, and very small polygonals can be distinguished, the latter of which lie chiefly along the manubrium of the hammer and towards the periphery, and contain the greatest number of the homogeneous spots. The color of the cells under the silver treatment is variable, some being scarcely at all colored, while others appear perfectly black and opaque; these latter are again found more frequently between the small polygonal cells. As is usually the case after the silver treatment, the nuclei become invisible, but occasionally a few of them can be seen, and then they usually have an eccentric position.

The fibrous framework of the mucous membrane lies under the above-described epithelium, between it and the membrana propria. The arrangement on the Human membrana tympani is variable; fig. 368 gives an idea of the form of this framework as most frequently found on the posterior segment of the membrane. Midway between the manubrium and the tendinous ring it is found as a membrane composed of the finest fibrillæ, which give off, in various directions, broad and narrow projections.

The membrane varies in size; on one side it reaches usually as far as the manubrium, and there passes into the mucous membrane, or else it stops at some distance from the hammer, and is then attached to the radial fibres by several projecting processes which interweave with them. I have usually also seen one process of the framework running to the short process

of the hammer. On the other side, that towards the tendinous ring, processes pass from the middle membranous expansion towards the periphery, and spreading out fan-like over the circular fibres unite with each other. These processes given off from the middle membranous expansion unite again near the periphery, thus forming openings which vary in shape, number, and position.

Fig. 368.

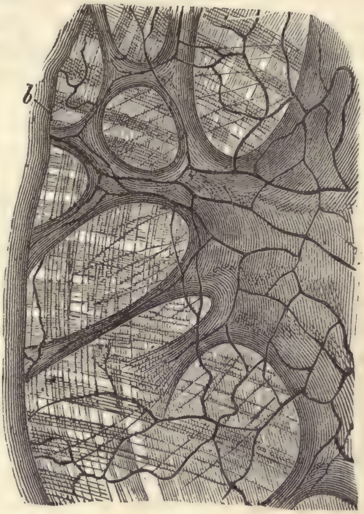

Fig. 368. A part of the posterior segment under slight magnifying power. *a*, the membrane, which is found directly under the epithelium, with its processes to the (*b*) tendinous ring. The dark-colored meshes correspond to the blood-vessels. A chloride of gold preparation.

The membranous expansion of this tissue also contains openings sometimes. The construction of the framework is complicated by the fact that all the described radial processes do not lie in one plane, but instead of going to the tendinous ring, pass deep in between the radial and circular fibres in the spaces already described, and there spread out as a system of ridges in such a way, that a number of these spaces communicating together form lacunæ. These lacunæ again may unite through openings between the circular fibres with the superior system of cavities. The described spaces are all lined with an endothelium which closely resembles, in its form and perishability, Descemet's epithelium of the cornea. By treatment with silver and chloride of gold dark-colored undulating lines appear in the form of meshes, such as are characteristic of the lymph vessels. In regard to the framework on other parts of the membrana tympani it should be said, that it normally forms on the anterior segment the same configurations as those just described, and is found as a perforated membrane only on the lower segments; yet here also the known variations in the arrangement of the fibres may appear.

Gruber, in a monograph, (8) describes a fibrous frame-work under the name of dendritic tissue, which, from its position, corresponds with the one we have described; its more intimate relations, however, have not been sufficiently appreciated by him.

On the edge of the mucous membrane for a space 0.220–0.088 mm. wide, especially in Children, villous processes, which were first described by Gerlach, are united with the fibrous frame-work. (On the pouch of Troeltsch and on the hammer these villous processes are also found.) They are covered by flattened epithelium, and are composed of connective tissue, in which capillary loops run.

Of the nerves, blood, and lymph vessels of the membrana tympani only the existence of the blood-vessels was known to Gerlach (7), v. Troeltsch (45), and Rüdinger (38). In regard to the nerves, v. Troeltsch (45) says that they are distributed chiefly and almost entirely in the cutis, but he does not describe their terminal endings; nor was he able to find them in the mucous membrane. Gerlach (7), however, several times recognized fine non-medullated nerve fibres in the mucous layer.

According to all who have yet investigated the anatomy of the membrana tympani, the membrana propria is destitute of nerves and vessels except on the periphery, where, according to Gerlach (7), there exists a capillary anastomosis between the mucous membrane and the cutis. No description of the lymph vessels exists, so far as I know, except that published by me in the *Centralblatt für medic. Wiss.* The result of my investigations shows that nerves, blood, and lymph vessels exist in the three chief layers of the membrana tympani, in the cutis, the membrana propria, and the mucous membrane.

The blood-vessels of the cutis and membrana propria are supplied chiefly by an artery which passes on to the membrane from the posterior and upper wall of the meatus, and descends on the posterior segment of the membrane along the handle of the hammer, sending off continually small branches in a radial direction toward the periphery. Toward the lower end of the handle it passes across the bone and divides into two branches, one of which supplies the lower anterior quadrant of the membrane. The branches running centrifugally in the cutis, and here and there united by transverse or oblique anastomoses, pass into a capillary network which, in some places, runs into the smaller veins accompanying the arteries, in others passes by the shortest course into two venous plexuses, one of which surrounds the handle of the hammer and empties its blood into the posterior superior veins of the cutis of the meatus, the other lies on the edge of the membrana tympani and discharges its blood also outward.

In addition to this chief artery, smaller ones at nearly equal distances pass in the cutis from the periphery on to the membrana tympani, divide rapidly into capillaries, and unite with those just described. The middle capillary network, which lies in the membrana propria, communicates both with that of the mucous membrane and with the external one just described; it expands between the radial and circular layers, and also in the system of cavities clinging closely to the walls of these latter at every point. On the middle and inner parts of the membrane, lying between the handle of the hammer and the tendinous ring, where the radial fibres in their course towards the manubrium are more and more crowded together, and where the circular fibres are wanting, the capillaries pass transversely or obliquely from the external capillary network between the radial fibres to the inner one of the mucous membrane, so that this portion of the membrana propria appears to contain the smallest number of vessels. Toward the periphery the radial fibres, here and there, separate from each other, leaving grooves which are filled by capillaries of rapidly increasing diameter, and which run like radii at regular distances. These capillaries also empty their contents into the peripheral plexus.

By separating the cutis and the mucous membrane from the membrana propria, the vessels passing through it transversely and obliquely are torn apart, so that the above-described spaces with their encapsuled nuclei can be seen.

The inner network of vessels of the mucous membrane consists chiefly of capillaries, and is distributed mostly around the handle of the hammer and towards the tendinous ring. The network in the latter place is to be regarded as a continuation of the capillaries of the tympanic mucous membrane. They pass on to the membrana tympani, bend in the form of loops round or else surround the openings of the ridge-work, and then pass back either to the vessels of the tympanic mucous membrane or to the edges of the tunnel-shaped passages, or directly deep down to anastomose with the capillaries of the membrana propria. The network surrounding the ham-

mer unites with the middle capillary network and also with that just described, receiving its blood from several small arteries which pass from above downwards nearly in the direction of the artery which runs in the cutis.

As we have just seen, the mucous membrane of the membrana tympani empties its blood in two ways, into the veins of the tympanum and into those of the external meatus. The chief volume of blood passing through the arteries and capillaries of the membrana tympani can, therefore, reach the larger veins by different courses, the shorter through the plexus of the hammer, the longer across the membrana tympani through the plexus of the periphery. Which of these ways is chosen by the blood during life depends evidently on the nature of the resistance which exists in the different parts of its course, especially in the veins. It may, however, be said with certainty that the arterial blood always passes back by the shortest course, through the plexus surrounding the handle of the hammer, when no special resistance exists in the veins into which the vessels of this plexus empty (Prussak, 37). I have convinced myself of the correctness of this latter view to which Prussak arrived by careful injections. As I cannot more minutely describe in this place the ways and means by which I arrived at this conclusion, I will content myself with giving the method which I used in demonstrating the course of the circulation in the membrana tympani. For this object I used Frogs treated with curara, the lower jaws of which by section of the masseters were drawn as far back as possible. Laying the animal between wet compresses on a plate of glass, in such a way that the external surface of the membrana tympani to be examined lay upon the plate, I then fastened the plate upon the object table of the microscope. On account of the short and wide Eustachian tube in the Frog, it is possible by an appropriate turning of the head in this way to study the circulation of the different parts of the membrana tympani very nicely.

Fig. 369.

Fig. 369. Lymph-vessels with their pouch-like expansions lying directly below the fibrous frame-work of the mucous membrane. Silver preparation.

In regard to the lymph vessels it may be said in general that they are arranged in three layers analogous to the blood-vessels; the first belongs to the cutis, the second to the membrana propria, and the third to the mucous membrane. In the cutis they form a very fine network, lying directly below the rete Malpighii, and which accompanies the blood capillaries at many points.

They pass gradually into larger capillaries, which often cross the blood capillaries and unite finally into independent larger branches, which either pass backwards and upwards, or, like the blood-vessels, pass at different points towards the periphery and the meatus. Sub-epithelial networks are found in the mucous membrane lying towards the tendinous ring, but only in small numbers; they are distinguished from the equally large blood capillaries by their numerous swellings. They pass through the holes described in the fibrous frame-work into the system of cavities, to form there large, round, and pouch-like expansions (*vide* fig. 369).

These latter expansions pass again into narrow capillaries provided with contractions which act like valves, and these capillaries unite with the deeper, tunnel-shaped branches, or else pass directly through the membrana propria, so that all three layers of the lymph vessels of the membrana tympani lie one below the other and unite with those in the cutis of the meatus. It should be further noticed here, that by brushing off the epithelium of the mucous membrane a lymph-canal system, like that first described by Recklinghausen (*vide* p. 219) on the diaphragm of the Rabbit, appears after treatment with silver, both on the membranes and ridges lying below the epithelium, and also on the depressions or tunnel-shaped passages lying between these. This canal-system, extending over the whole membrana tympani, is most distinct, however, on those spots covered by the small-celled epithelium of the mucous membrane, along the handle of the hammer and towards the tendinous ring; the clear spots, which frequently unite together, here increase in number and extent at the cost of the brown-colored masses.

Fig. 370.

Fig. 370. Serous canaliculi of the membrana tympani of the Dog.

On the membrana tympani of the Dog and Cat I found, as in Man, that where the light spaces existed, fine, very undulating lines, which were here and there somewhat thickened, and which became by continuous division finer and finer, stretched in all directions even into the brown masses (*vide* fig. 370). Similar appearances of the lymph-canals were described by Koester (*Ueber d. feinere Structur d. menschl. Nabelschnur*. Dissert. inaug. Würzburg, 1868), on the placental cord, and by him used as a support to his theory that the lymph-canals were formed of epithelial cells. Here and there the light spaces are seen accompanying the contours of the vessels; they then run on one or both sides along the vessels and communicate with the points of neighboring lymph-canals. In what relation the lymph-canal system stands to the epithelium of the mucous membrane, or rather to the openings described in it, I have not as yet been able to discover, and will here only state the interesting physiological fact that I

have been able, in the Dog, to fill the lymph-vessels of the membrana tympani most beautifully and completely from the tympanum by the method first used on the diaphragm by Recklinghausen and afterwards by Ludwig and Schweigger-Seidel. From these injections and from the described arrangement in the system of lymph-vessels we might suppose that every alteration of tension of the membrana tympani would cause a suction on the contents of the tympanum, and finally force it forward within the lymph-vessels.

The nerves of the membrana tympani are distributed like the vessels in the cutis, the membrana propria, and the mucous membrane. The larger nerve trunks accompany the chief vessels, divide as these do, and frequently unite together like the capillaries. They are distributed with the latter and form thick networks under the epithelium of the cutis, and also under that of the mucous membrane. A fundamental plexus, a capillary plexus near the vessels, and a sub-epithelial plexus may be distinguished.

The chief nerve trunk, consisting of medullated fibres provided with a sheath of Schwann, lies on the boundary between the cutis and membrana propria; it passes from the meatus on to the membrana tympani at the upper part of the posterior segment close to and behind the artery, and distributes fibres which accompany the twigs given off from this artery. At the end of the handle of the hammer the nerve divides into two branches corresponding to the division of the artery, one of which supplies the anterior and the other the posterior and lower parts of the membrana tympani. Besides this chief trunk, several small branches enter the membrane with the blood-vessels at different parts of the periphery. The coarser of these nerves, lying on the boundary of the cutis and membrana propria, I call the fundamental plexus of the membrana tympani. The twigs given off from them divide into numerous non-medullated fibres with sheaths, and then form numerous plexuses around the vessels, and also in the spaces between the capillaries. Examining more minutely such a plexus which accompanies the vessels, we see single nerve fibres clinging close to the contours of the capillaries, and here and there separating again from them, so that a small clear space becomes visible between the nerve and the wall of the vessel. In its further course the nerve may leave the vessel and join the plexus found directly under the rete Malpighii, or it may separate directly into minute fibres which are woven around the capillaries.

Lippmann (*Inaug. Dissert.*, Berlin, 1869) and Thomsa (*Centralblatt*, Nr. 39, 1869) have described this same appearance, but they were unable, however, like myself, to discover the closer relation of the nerve threads to the nuclei of the capillaries.

A second variety of nerve fibres is of a different nature from those just described, showing a simple axis cylinder which at many points passes into coarse swellings with distinct nuclei. From one such swelling two or more fibres may be given off, and in the latter case it has the appearance of a small ganglion cell. On successful preparations I have seen such fibres coming in close relation both with the cells of the rete Malpighii and also with the vessels lying directly below it, the fibres with their nucleated swellings lying on the capillaries as above described, and again separating from them (fig. 371).

At other points the nerve fibres may be traced into fine threads which in their further course show frequent pear-shaped swellings. These latter appear dark-colored after treatment with chloride of gold, while the neighboring nuclei of the capillaries usually remain lighter. On gold prepara-

tions it has the appearance as if the pear-shaped swelling lay in the angle of a forking nerve, one of whose prongs comes to a knob-shaped end in the immediate proximity of the swelling, while the other becomes lost in the wall of the capillary vessel in a manner as yet unknown (fig. 371, *d*).

Fig. 371.

Fig. 371. Nucleated nerve fibres which, with their pear-shaped swellings, lie on the wall of the capillary at *d*. Chloride of gold preparation of the Human membrana tympani.

As yet there is no reason for considering these swellings as the terminal endings of the nerves of the vessel, since threads are given off from them which are lost on the wall of the vessel. The described relations can only in rare cases be seen satisfactorily, because the long course of the nerve fibres before their division into fine threads seldom allows their connection with the pear-shaped swellings to be seen.

It was said above that only one portion of the nerve fibres was connected with the vessels, while another portion united with the plexus lying in the rete Malpighii. This latter forms a network provided with bi-polar or multi polar cells which are directly under the deeper layer of the cuticle. From this network very fine but distinctly recognizable threads pass off; these often run directly between the cells, so that we may be in doubt whether we have to deal with the cell boundaries or with such threads, but they frequently also pass over both the cell boundaries and the nuclei in order to reach the neighboring or more superficial cells. I am unable to assert anything positive in regard to their termination.

It should be stated here that numerous nerve fibres from the fundamental plexus pass in between the fibres of the membrana tympani in order to reach the membrana propria, where they are seen to lie either on the tendinous fibres, or to pass through the slits and holes between these fibres to join the nerves of the mucous membrane. In the course of distribution of these fibres, nucleated swellings of the nature already described are found on the finer fibres.

We find therefore in the membrana propria the openings for the vessels with the contents as described, and in addition to these a large number of nucleated swellings provided with two or more processes which unite with the nerve fibres, and which lie above and between the single fibrous layers. I state these facts once more, because as yet all the cell elements found between the fibres of the membrana propria were considered as belonging to the connective tissue, while in reality only a small part of them belong to this tissue, as the above description shows, and the greater part must be considered as belonging to the blood and lymph vessels and the nervous system.

Finally, in regard to the nerves of the mucous membrane of the membrana tympani, I must insist that they are by no means as seldom met with as has been heretofore supposed. Here also a plexus is found near the vessels, and also a sub-epithelial plexus. The former, accompanying by

preference the lymph rather than the blood vessels, receives its fibres partly from the plexus tympanicus by threads, which pass on to the membrana tympani with the mucous membrane of the tympanum from different points of the periphery, partly from those nerves which lie in the cutis by threads coming through the membrana propria. It sends its twigs on the one side to the blood and lymph capillaries, on the other to the sub-epithelial plexus. The latter forms a fine network directly under the epithelium, which it supplies with threads.

B. The Middle Ear

includes 1, the tympanum, with the ossicles and their muscles and ligaments; 2, the cells of the mastoid process, and 3, the Eustachian tube.

The Tympanum.—The osseous walls of this cavity, the structures which are found in it, and the inner surface of the membrana tympani are all covered by a mucous membrane, a continuation of that lining the Eustachian tube, which also passes through the antrum mastoideum to line the cells of the mastoid process. The mucous membrane of the Human tympanum is composed chiefly of an epithelium and a layer of connective tissue beneath it.

The epithelium varies in its form; on the floor of the cavity and also on the anterior inner and posterior walls it consists chiefly of ciliated columnar cells; on the promontory, roof, membrana tympani, and ossicles of pavement cells (Troeltsch). The change from one form to the other is gradual; the ciliated columnar cells becoming lower, passing into ciliated pavement cells, and finally into pavement epithelium destitute of cilia. By separating the columnar epithelium and isolating the cells, chalice-like cells, like those in the mucous membrane of the intestine, and ciliated columnar cells, with and without nuclei, are found; these latter without nuclei have an extremely small, often rod-like body, and a few cilia which are frequently glued together. Both the chalice-like and the columnar cells pass at their lower ends into a homogeneous, glistening thread, and sometimes they divide and connect with two such threads. On one preparation I have been able to isolate a cell with two processes, one of which remained in connection with a thread three times the length of the cell itself, and which could be followed for some distance into the connective tissue. By moving the covering glass, the cell with its thread attached floated free in the surrounding liquid, so that there was no doubt of the connection here described. Rüdinger has also described threads on the mucous membrane of the Eustachian tube, which are connected at one end with the epithelial cells and at the other with the submucous tissue. Besides the above-described forms of columnal cells a second spindle-shaped form is found, characterized by a nucleated cell-body from which processes are given off in two directions, upwards and downwards. The upper process reaches into the epithelial region, while the lower one passes into a bright glistening thread which is lost in the underlying tissue, and which frequently, not far from the point where it leaves the cell, is provided with a coarse nodosity. In examining the flattened epithelium, wherever found, it shows the same peculiarities of form already described on the epithelium of the mucous membrane of the membrana tympani. By removing the epithelium and then treating the mucous membrane by the silver method, lymph canals are seen; if, however, the epithelium is not removed, but the intact mucous membrane treated with a solution of chloride of gold or perosmic acid, dark or black star-shaped figures, communicating with each other, are seen directly under the epithelium; these figures here and there pass into broad dark-colored streaks

which run into the deeper layers of tissue. Whether these latter figures are to be considered as identical with those brought out by the silver method, and whether they stand in any closer relation with the lymph vessels, must remain an open question, as I cannot bring forward a decided proof of their identity.

In the connective tissue which underlies the epithelium two layers can be distinguished, an upper, lying under the epithelium, and a lower, corresponding to the periosteum, which gives off some fibres to the sheaths or the nerves which run in the depressions in the bone, and some also to the tunica adventitia of the blood-vessels of the bone. The upper layer forms a fibrous frame-work, a continuation of that already more minutely described on the membrana tympani, and bears the same relation to the periosteum as that does to the membrana propria. It is composed of the finest fibrillæ, which together form a frame-work of ridges and perforated membranes, enclosing larger spaces filled by nerves, blood, and lymph vessels. On different points of the tympanum this fibrous frame-work separates from the periosteal layer, and passes from one projection of the bone to another, through the free space of the cavity. These bridges serve both as supports for numerous capillaries passing from one point to another, and also for an epithelium which is continuous with that of the mucous membrane. The ligamentum mallei superius, lig. mallei externum et posterius, and the posterior pouch of the membrana tympani are formed by such bridges. The lig. mallei anterius consists of a thick bundle of fibrillæ resembling tendinous tissue, and constitutes with the lig. mallei posterius the so-called axis-cord which forms the axis of the hammer (Helmholtz, 11). The ridges which stretch across between the numerous bony projections on the floor of the tympanum should be mentioned here. One frame-work of ridges which I have frequently observed in the neighborhood of the stapes deserves special mention; it passes from the eminentia pyramidalis over to the semi-canal of the tensor tympani as a bony ridge—sometimes projecting far into the tympanum—and forms, with the posterior upper wall of the cavity, a more or less deep niche. From the free edge of this ledge I have frequently seen several ridges, often one above the other, which stretched across the niche and were inserted on the base or posterior arm of the stapes. On these ridges, as well as on those on the floor of the cavity, and also on those passing from the roof of the cavity to the head of the hammer (lig. mallei superius) *peculiar bodies* exist, which, although differing from each other in external form, show the same histological construction. In the simpler forms of these an axis band can be seen running along the centre, and surrounded by concentrically arranged capsules. This axis band forms a flat or round cord which, running free for a longer or shorter space, passes finally into one pole of a lemon-shaped body, passes out at the other pole, and immediately spreads fan-shaped into the perforated membrane already described in the mucous membrane. Without the addition of coloring matter it can be seen to have a very fine fibrillary structure, and between the fibrils an opaque finely granulated mass; treated with a solution of silver or chloride of gold, however, it is colored more strongly than the tissues of the capsules. The capsules which surround the axis band concentrically also have a fibrillary structure. Between the different capsule-layers are spaces which appear either homogeneous or filled with spindle-shaped elements; the edges of these spaces are frequently covered with a finely granulated opaque mass. The outermost capsule layers are often undulating on their external surface and possess a delicate flattened epithelium. The capsules form at one pole of the body a round glistening ring, with a tunnel-shaped depression, where

the axis band enters; at the other pole the capsule passes into the axis band. This description answers for the simple forms which, except for the structure of the axis band, resemble in appearance a Vater's corpuscle. In addition to these simple forms just described, these bodies may be so contracted as to resemble the figure 8, or they may be bent at any angle; in either case they have the appearance of two of the bodies so united together that at the point of union the corresponding capsule-layers passed into each other. Sometimes an axis band after its exit divides into numerous branches on which are the same but smaller bodies. Fig. 372 shows one of these bodies which I found between the base of the stapes and the ridge stretching from the eminentia pyramidalis. These same organic structures are found also on the mucous membrane of the mastoid cells, as we shall see later, but they never reach there such a marked size as in the tympanum. They may be round, oblong, or spindle-shaped, and are found of all sizes, from 0.08–0.5 mm. in length.

Although I am unable to define the histological signification of these bodies, nevertheless, their presence on the ridges, and the close union of these latter with each other, and with the sound-conducting apparatus of the middle ear, would seem to show that they take some part in the physiology of hearing, the more accurate determination of which must be left to experimental physiology.

Fig. 372.

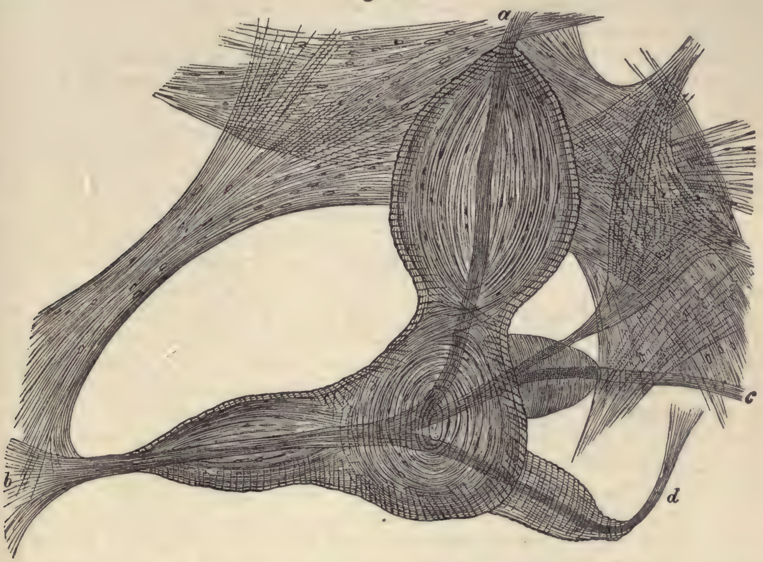

Fig. 372.—*a*, entrance of the axis band; *b*, its change into a membrane; *c* and *d*, branches of the axis band with smaller bodies.

These bodies were first described as pathological formations on the tympanic mucous membrane of an old deaf woman, by v. Troeltsch (Virch. Arch. Bd. vol. xvii. p. 60, 1859); their signification as physiological structures was first determined by myself (19 and 21) and Politzer (34 and 35).

The tympanic mucous membrane is nourished from both sides, receiving its blood from different sources. The chief artery winds along the floor and over the promontory; the branches given off from it form round or elliptic loops

along its course and then pass into a capillary network under the epithelium, which empties its blood through a capillary venous system of rapidly increasing calibre into the quite large veins of the periosteum. All of the arterial branches, however, do not take this course; some run without dividing and stop suddenly in the capillaries, which—often in large numbers and equally distant from each other—pass in between the fibres or the perforated membranes and pour their blood into the large veins.

The lymph-vessels of the tympanic mucous membrane closely resemble those on the membrana tympani; in Man they form here and there a system of tubes, which run chiefly in the periosteum, and which have globular enlargements or strongly-marked lateral projections; or else they spread out as pouch-like enlargements in the cavities of the fibrous framework. This tubular system does not exist in all parts, however, but here and there, as on the upper osseous wall and roof of the tympanum; it is converted into funnel-shaped or round cavities communicating together and penetrated by a fine network. Such a formation is found on the tympanic mucous membrane of the Dog, and will be more minutely described hereafter. I found these cavities frequently filled with white blood-corpuscles, giving one the impression of follicles. The observation of Thasiloff, in which he claimed to have found a lymph-gland in the tympanic mucous membrane, at the junction of the upper wall of the cavity with the membrana tympani, probably depends on this appearance. As to the possible relations of the lymph-vessels to the epithelium of the mucous membrane, I cannot go further than the conjectures already given, in regard to the figures which appear under the epithelium after treatment with silver and chloride of gold.

The nerves which are distributed in the mucous membrane of the tympanum and the membrana tympani, and which can also be followed into the membrane of the Eustachian tube and the mastoid cells, arise from the tympanic plexus, which is an anastomosis between the ganglion oticum, the ganglion petrosum nervi glosso-pharyngei, and the plexus caroticus or ganglion cervicale superius nervi sympathici (Bischoff, 3).

The chief nervous branches of the tympanic plexus consist of medullated fibres, which run in the periosteum of the lower and inner wall of the tympanum, and give off small branches to the superior layer of connective tissue lying just below the epithelium. These branches form, by numerous anastomoses with each other, broad irregular meshes, and from these anastomoses non-medullated fibres are given off, which form a fine network directly beneath the epithelium. Encapsuled ganglion-cells, of variable diameter, single or in groups, lie upon or are embedded both in the chief nerve-trunks and also in their branches: these ganglia are found not only along the course of the nerves, but also at their points of division. I am, therefore, able to confirm the assertions of Pappenheim (32), Kölliker (22), and Krause(23), in regard to the extensive distribution of the ganglia, in opposition to E. Bischoff (3), who said that they were confined to one branch only which ran from the nervus tympanicus. I should add here that in the Dog and Cat I have found single ganglion-cells, provided with sheaths, lying close under the epithelium of the mucous membrane, where the fine network already described is situated.

The mucous membrane in the Dog and Cat is analogous in its formation to that of Man. The epithelium has the same forms as in Man, and beneath this is a fibrous framework corresponding to the periosteum, as has been already minutely described. The chief nervous branches show, in some places, thimble-shaped swellings, and in others deep furrow-like contractions caused by glistening bands. Large numbers of ganglion-cells are often embedded in

and upon the nerves, and I found such ganglion-bearing branches directly under the cylindrical epithelium. On the side towards the nerves these columnar cells gave off small processes which could be followed into the nerve-sheath, but in regard to their final termination I am unable to state anything more definite.

The nerves themselves have another remarkable characteristic, viz.: I have been able by injections to prove the existence of capillary blood-vessels, which form a minute, basket-like plexus, both in the nerve-sheaths and also between the nerve-fibres: this system of blood-vessels can also be made apparent by the chloride of gold method. By treating injected preparations, which have been previously hardened in alcohol, with chloride of gold, a second system of tubes which are not filled with the injection will be made apparent; this usually accompanies the nervous sheath or lies in it, and is distinguished from the system of blood-vessels by the existence here and there of round or spindle-shaped enlargements, which are characteristic of the lymphatic system. I have been able to follow branches of this system through the nerve-sheath into the nerve-fibres, but the distribution in the nerve itself has up to this time escaped my observation.

Von Troeltsch's (44) assertion, in regard to the existence of mucous glands in the Human tympanum, remains as yet unconfirmed; their existence, however, in the Dog and Cat I have determined satisfactorily: in these animals they are glands with a single duct, and with a lining of columnar epithelium.

The further disposition of the nerves and lymphatics in the tympanum corresponds exactly with that in Man; I desire only to direct attention to the mucous membrane of the bulla ossea. Here the mucous membrane alters its character; the medullated nerve-fibres, surrounded with sheaths and ly-

Fig. 373.

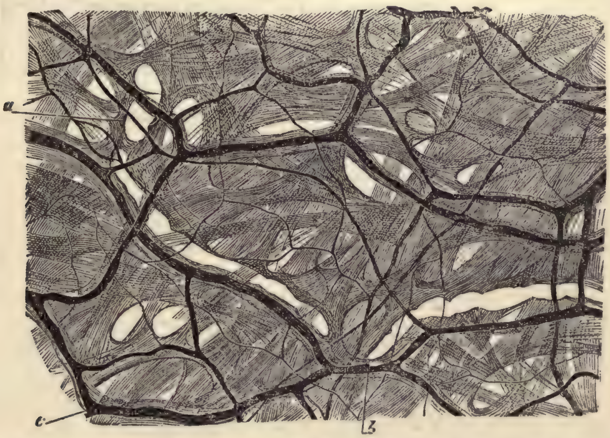

Fig. 373. Mucous membrane from the bulla ossea of a Dog. In the tissue, spaces are visible which at *a* and *b* pass into lymph canals. *c*, blood-vessels filled with a glutinous mass. A chloride of gold preparation.

ing directly under the epithelium, become less frequent, and the ganglion-cells correspond in form and appearance with those in the tympanum proper. By separating the epithelium from the very thin layer of connective tissue lying beneath it, an adenoid network is found, which, in some places,

is very thick and has groups of large openings. These openings lead into funnel-shaped or round spaces, which communicate with each other through holes in the tissue, and finally become tubes of variable width.

These spaces are again crossed by a fine network, and are lined by a very delicate epithelium; they are sometimes empty, sometimes filled with lymph corpuscles; large and small drops of fat are also almost always found in them. By the addition of a solution of perosmic acid, these latter are colored black, and the course of the tubes and the position of the spaces is brought out sharply. I have also seen fat globules in the veins. Injections from the aorta do not pass into these spaces and tubes even when the blood-vessels are perfectly filled: from this circumstance, and from their form and contents, we are justified in considering them as belonging to the lymphatic system.

I have sought in vain in the literature for descriptions of the lymphatic vessels of the tympanum; Prussak, (37) who undertook minute investigations of the tissue in the Dog, denies their existence entirely. From the manner in which the numerous larger veins are formed from the capillary network, from the direct passage of the smaller arteries into the veins, and from the simultaneous discharge of the large veins at different places, the stream of blood should pass with slight pressure and great rapidity through the vascular system, and should not favor exudations which might otherwise be expected from the slight density of the tissue separating the blood-vessels from the tympanic cavity, and from the absence of lymph-vessels. Although the arrangement described by Prussak can be recognized in the blood-vessels of the mucous membrane of the Dog, the chief reason for the non-appearance of such exudations is to be sought in the existence of the lymph-vessels: in fact, it is easy to satisfy one's self that the resorbent surfaces of the lymph-vessels exceed those of the blood-vessels. The lymph vessels lie in the described system of cavities directly under the thin, elastic, and easily compressible membrane, and in considering the question of their action we should remember the principles generally applicable to the movement of lymph, and also the frequent changes in pressure which take place in the tympanum, since these variations in pressure appear well adapted, from the mechanism of the lymph-vessels, to suck the fluids of the tympanic cavity into the lymph-vessels and to force it forward after entering them. The assertion of Voltolini, (46) that a small quantity of clear fluid is always present in the Human tympanum, applies equally well to the mastoid cells, where I have also found it.

Peculiar cellular bodies deserve special mention, which lie chiefly in the deepest layer of the periosteum of the bulla ossea, close to and between the blood and lymph vessels lying in it, but also pass through the superficial layer of connective tissue to the epithelium. These bodies consist of a disk-shaped, round, or oblong cell with several processes. This cell-body shows usually a large nucleus with a distinct nucleolus, or, under certain circumstances, many such nuclei, which again have several distinct nucleoli. There is usually among the 2–5 small processes one that is larger than the rest. The larger usually runs for a longer or shorter distance, and then unites with a second similar cell-body; this again gives off processes which anastomose with others, thus forming a plexus. The smaller processes divide into branches, and finally into fine threads which, under favorable circumstances, can be seen to unite with nucleated cells. Both the body of the cell and its processes appear finely striated and covered by a finely granular mass, the former more so than the latter. The cells with a single nucleus resemble in their form the ganglion cells of the spinal cord, those with several nuclei resemble closely the myeloid cells. Probably the appearance of the latter is caused by the multiplication of nuclei, but the change of the disk-shaped cells into spherical is undoubtedly owing to this cause.

Before leaving the tympanic cavity, a few words are necessary on the ossicula, their union with each other, and the muscular apparatus attached

to them. The ossicula are covered by a mucous membrane, and in adults by a very thin periosteum; they have a compact external and a spongy internal substance. The latter is crossed by numerous vessels which pass through the compact substance and unite with the periosteum and the vessels of the mucous membrane. On the head and neck of the hammer and on the body of the anvil the spongy substance is increased at the expense of the compact substance, while on the long and short process of the anvil and on the handle of the hammer the opposite takes place. The articulating surfaces of the ossicula resemble other true joints; they have capsules and a layer of hyaline cartilage on the articulating surface.

The insertion of the stirrup in the fenestra ovalis will be more minutely described with the tissues of the vestibule.

The muscles of the ossicula are striated and covered with mucous membrane wherever they pass through the tympanic cavity. The tensor tympani muscle is connected with the dilatator tubæ not only by tendinous fibres, as Majer (27) thought, but also by muscular fibres, as has been already described. At the point of insertion of its tendon on the hammer cartilage, cells are inserted.

Cells of the Mastoid Process.

The mastoid cells are lined by a very thin mucous membrane, a continuation of that in the tympanum, which has in general the same anatomical structure as in that cavity. Its epithelium consists of smooth cells of the same consistency and arrangement as those more minutely described on the membrana tympani. Under this an upper and a lower layer of connective tissue corresponding to the periosteum is met with, the lower layer containing numerous nerves, blood and lymph vessels. The upper layer of connective tissue frequently separates in the form of membranes on the free edges of the cells, and passes over to neighboring projections of bone and is there inserted, so that in this way frequently the cavities of two neighboring cells are separated from each other. In the larger cells these membranes are stretched horizontally like curtains by means of processes which arise from them. On the ridges of the membrane the concentrically arranged organs already described are frequently found (I have counted as many as seven). They never here reach as great a size as those in the tympanum, but are much richer in interesting forms; they vary in size, from the smaller spindle-shaped forms to the larger round, club-shaped, and flattened forms. I have frequently found membranes with their processes and the bodies attached to them in the aditus ad cellulas,* and have also seen the processes in direct union with the short process of the anvil.

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* Antrum mastoideum? Transl.

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II. THE EUSTACHIAN TUBE.

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In the different animals and in Man the Eustachian tube is formed on a peculiar morphological plan, by a modification of the elements of its various structures.

Although the resemblance of the different portions of the tube in different animals is close, yet their minute differences of form appear so characteristic, that from a section of the Eustachian tube the animal from which it is taken can be designated.

As a mechanical apparatus composed of cartilaginous and muscular structures, the tube is closely related physiologically to the tympanum. In addition to conducting away its own secretion and that of the vascular mucous membrane of this cavity, it is also able to produce a ventilation of the cavity by means of the mechanism which it contains.

Whether the Eustachian tube plays an important physiological rôle in the conduction of sound in the tympanum, and whether it has any connection with the voice, and if so, what this is, cannot be satisfactorily answered from the study of its comparative morphology. The final determination of these questions must remain for experimental investigations.

1. The osseous and cartilaginous tube.

The osseous Eustachian tube in Man forms a long triangular fissure, the greater diameter of which lies almost perpendicularly. The base of the triangle, which is directed upward, is bounded by a thin lamella of bone, which sometimes completely separates the tube from the round semi-canalis tensoris tympani. When this bony lamella is broad, it bends anteriorly somewhat upwards, so that the upper end of the tube has a less diameter and lies in front of the osseous semi-canal. The medial opening of the osseous tube, at its point of union with the cartilage, is jagged and oblique, the bone on the medial side passing farther back than on the lateral side of the tube, and this fact should, as Henle has stated, be remembered in considering the insertion of the cartilage in the bone.

If cross-sections are made on a temporal bone carefully deprived of its lime, and with which the Eustachian tube still remains connected, beginning through the medial section of the tympanum, and then here and there down the tube, so that the sections fall at right angles to its long axis, we can see the gradual transition of the tympanum into the osseous tube, and the relations of this latter to the cartilaginous tube.

From this it is seen that the tubal cartilage, which sinks into the jagged ends of the bone, forms a simple prolongation of the walls of the osseous tube; the hyaline cartilage, however, which forms the tube, is not united directly with the bone, but a fibrous cartilaginous tissue is inserted between. This fibrous tissue passes into the hyaline cartilage, and from this fact, C. F. Th. Krause was led to think that the upper end of the tube was fibrous cartilage. It must be granted that the two varieties of tissue on this spot do not appear sharply defined, since the fibro-cartilago basilaris also passes here and there into the tubal cartilage.

The cartilage in the neighborhood of the osseous tube has the form of a thin plate, bent at right angles, with a horizontal portion, and a thinner, perpendicular, lateral portion. On the medial side there is no cartilage,

because the medial posterior wall of the osseous tube is longer than the lateral, and hence at this point the medial side is formed by bone, while on the opposite side the lateral cartilaginous plate appears.

From these cross-sections it is further evident that the transition of the osseous into the cartilaginous tube is a very gradual one. At some distance from the osseous tube cartilage cells, at first single and then in greater numbers, are found in the dense fibrous tissue. The hook-shaped cartilage of the Human Eustachian tube, which is attached to the base of the skull by means of the so-called fibro-cartilago basilaris, is quite thick, and consists of a non-vascular hyaline cartilage, as Kölliker has said. Its hyaline substance is crossed by a few fibres and encloses island-like groups of round and oval cartilage cells of different sizes, the larger of which contain two or more nuclei, the smaller only one. Towards the surface the cartilage cells become gradually smaller, and a layer of nucleated connective tissue, corresponding to the perichondrium, is found. Between the perichondrium and

Fig. 374.

Fig. 374.—Transverse section of Eustachian tube and surrounding parts. 1, median cartilaginous plate; 2, lateral cartilaginous hook; 3, musculus dilator tubæ; 4, musculus levator veli palatini; 5, fibro-cartilago basilaris; 6 and 7, acinous glands; 8, deposit of fat in the lateral wall; 9, safety tube; 10, accessory fissure; 11, fold of the mucous membrane; 12, adjacent tissues.

the true substance of the cartilage no sharp boundary line exists, but the one variety of tissue passes gradually into the other. This connective tissue, which furnishes a passage to the vessels, passes at some points more or less deeply into the cartilage substance, so that it forms on cross-section island-like groups, which in cattle enclose small acinous glands. On the lateral blunt end of the cartilage-hook the fibrous layer is thicker than on other parts, partly owing to the fact that the tendon of the mus. dilatator tubæ is inserted here.

In the Quadrumana, and also in the Volitantia, the cartilage of the Eustachian tube more closely resembles the true hyaline variety than it does in Man, since the fibrous substance, particularly in the Bats, nearly disappears, and the hyaline substance is found with quite large cartilage cells.

This is also true of the Eustachian tube in the Rodentia, the Pachydermata, and Ruminantia. In the latter, the scattered cartilage cells are small, and the whole cartilage appears composed of several pieces. The external form of the cartilage also varies in a marked degree in the different animals. In the Talpa Europæa, Arctomys marmota, Canis vulgaris, Mustela martes, and Lutra, it forms either a simple cartilaginous lamella or a cylindrical rod on the medial side of the tube: in the Lutra deposits of lime are embedded in it. In the Dog, Martin, and Otter the tissue surrounding the cartilage consists of layers of connective tissue mixed with elastic fibres. In the Felis domestica, Felis leo, Felis tigris, the cartilage is confined to one end of the tubal fissure, and has the form of a hook. The remaining portion of the tube in all of these animals is enclosed by interweaving fibrous tissue which on the medial side contains small cartilaginous lamellæ.

In the tubal cartilage of Man I have observed several times a high degree of fatty infiltration, from which it appeared in all its measurement two or three times larger than normal; each cartilage forms projecting swellings on the wall of the pharynx.

2. The Muscular (Membranous) Portion.

I have already said that the designation membranous portion of the tube was an uncertain one, since it suggests the mucous membrane, which by no means belongs to one portion of the Eustachian tube, but exists throughout its whole extent, and is united both with the cartilage and the muscles. It might, however, be retained without particular disadvantage if the use of the expression was once fixed to designate that portion of the tube not surrounded by cartilage; such a limitation of the term would be particularly applicable to the Eustachian tube of some animals. Nevertheless, if we are not inclined to be particular in retaining this name, it would be advantageous to give up this designation for Man and many animals, and to call that portion of the tube of which we are speaking the muscular portion.

I am well aware that we have to deal here with muscles which do not belong alone to the tube, and that the morphological nature of this portion of the tube is not exactly expressed by this name. There is no absolute reason, however, that the nature of the tissue should be expressed in the name, and it seems to me there is no other resource except to name this portion from the muscles which are in such close morphological and physiological relation to it.

As I consider the layer of tissue between the muscles and mucous membrane as the sub-mucosa, we have in a histological point of view only a few points to speak of in regard to the muscular portion of the tube. In order to understand perfectly the relations of the voluntary musc. dilatator tubæ to the cartilage, cross-sections must be made through the tube, with its osseous surroundings, which have been previously deprived of lime, and these sections must be made in such a way that they shall run parallel with the muscular fibres. On such sections, which may be quite thick, it is seen that the musc. dilatator tubæ is without doubt inserted only on the blunt end of the cartilaginous plate along the whole length of the Eustachian tube. Its flat tendon is bounded in the Human tube by the sub-mucosa, and receives on its outer side the striated muscular fibres; as it passes upwards it unites

with the perichondrium of the end of the hook. There is no doubt that in the Human tube the dilatator tubæ shows no direct transition into the mucous membrane. Even in those cases in which there is an appearance as though the muscle united with the mucous membrane in the neighborhood of the cartilage, still cross-sections show that an isolated bit of cartilage is connected with the point of the hook by means of dense tissue.

That a direct transition of the musc. dilatator tubæ into the tensor tympani takes place, as v. Troeltsch and L. Mayer state, I have been able to confirm, not only in regard to the tendons, but also the striated muscular fibres of both muscles, both on cross-sections and from surface views. The muscular portion of the tube in Apes is strongly developed, particularly the musc. dilatator tubæ, which is only attached to the blunt end of the lateral cartilaginous plate. I have deprived the bones of an Ape's head of lime and, making sections through the tubes and their surroundings, have found that the musc. dilatator tubæ does not pass beyond the limits of the lateral cartilage. The muscles bear this same relation to the cartilage in the Hog, the Horse, the Red Deer, the Fallow Deer, etc.; an exception to this arrangement is found in those animals in which no cartilage exists on the lateral side of the Eustachian tube, such as the Woodchuck, the Dog, Martin, Lutra, and Cat.

In these animals the dilatator tubæ is directly connected with the dense sub-mucous tissue. I should state that in the Horse two voluntary muscles, the so-called levator and tensor palatini, pass into the lateral portion of the cartilage.*

The musc. levator veli palatini bears a peculiar topographical relation to the Eustachian tube, since it passes up to the pars petrosa on the floor of the tubal fissure close to the mucous membrane, and is attached not only on the bone, but also with some of its fibres on the thickened sub-mucosa of the mucous membrane.

On the Eustachian tube of the Red Deer a special striated muscle exists, which is attached on the medial side of the tube. In the Stag it is strongly developed. Its separate bundles, surrounded by fat, pass to the medial mucous membrane, and form a close union with this, its tendon being continued directly into the fibrous layer of the sub-mucosa. It serves to fix the mucous membrane, which is destitute of cartilage, and I have named it dilatator tubæ medialis.†

3. The Mucous Membrane.

The mucous membrane of the osseous Eustachian tube, which sinks to variable depths into the uneven surfaces of the bone, varies in thickness between 0.080–0.112 mm. On cross-sections through the osseous tubes no boundary between the periosteum and the mucous membrane can be recognized. A finely fibred nucleated connective tissue is in close union with the substance of the bone, and from it processes pass into the interior of the bone. At a short distance from the bone the connective substance becomes somewhat looser, and encloses a coarse network of vessels which are distributed not only in the mucous membrane but also in the substance of the bone. It reaches a marked consistency in the neighborhood of the projecting bony ridges, and also on the floor of the osseous tube, where, on cross-section, larger or smaller vessels are met with, which here and there pass to

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* Rüdinger, *Beiträge zur Anatomie und Histologie der Ohrtrompete.*

† Rüdinger, loc. cit. Figs. 42 and 43.

the cartilaginous tube. At some points the basal membrane, with its ciliated epithelium, joins the loose sub-mucosa. At other points of the mucous

Fig 375.

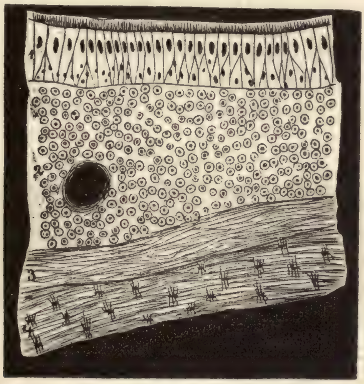

Fig. 375. Section of the osseous Eustachian tube. 1, ciliated epithelium in several layers; 2, conglobulate gland substance; 3, periosteum; 4, bone. $\frac{184}{1}$.

membrane, most frequently under the osseous lamella, which separates the Eustachian tube from the semi-canalis tensoris tympani, thickly crowded

Fig. 376.

Fig. 376. Section of the upper third of the Eustachian tube. 1, medial cartilage; 2, lateral cartilage hook; 3, perichondrium; 4, sub-mucosa; 5, insertion of the dilatator tubæ; 6, safety tube; 7, lateral projection of the mucous membrane 8, medial projection of the mucous membrane; 9, accessory fissure. $\frac{184}{1}$.

lymph corpuscles are found in a finely fibred reticulum, and we have here before us the layer of tissue which in the pharynx and intestine has been described as conglobulate gland substance. It forms a layer varying in thickness from 0.040–0.056 mm., and lies next the basal membrane with its ciliated epithelium (*v.* fig. 375). This basal membrane has a thickness of 0.028 mm.

The pale thin-walled vessels remain to be described, which, net-like, pass through the sub-mucosa, and, in sections of injected preparations, are found to contain none of the injected mass, so that we are compelled to consider

Fig. 377.

Fig. 377. Section from the upper third of the Human Eustachian tube. 1, 2, cartilage; 3, musc. dilatator tubæ; 4, lateral sub-mucosa; 5, medial projection of the mucous membrane with its vessels; 6, lateral projection of the mucous membrane with its vessels; 7, large vessel on the roof of the tube; 8, safety tube with the mucous membrane; 9, accessory fissure. $\frac{184}{1}$.

them lymph vessels. All the other large openings and fissures which in the submucosa communicate with each other appear on such preparations as blood-vessels. On the floor of the osseous Eustachian tube fine folds of variable form are found, such as I have already described in another place, and on section these appear as villous projections.

In the cartilaginous portion of the Eustachian tube the mucous membrane and the space enclosed by it varies in many points from that described in the osseous portion, as acinous mucous glands, and peculiar folds are found here which are closely related to the mechanism of the tube.

In the Human adult I have distinguished two portions in the tubal fissure. I have named the semi-cylindrical space under the hook of the cartilage *safety tube* and the fissure connecting with it the *accessory fissure.* These

two designations best express their physiological use. Both divisions are produced by the configuration of the cartilage, and are separated from each other by projections of the mucous membrane. While on the concavity of the hook the mucous membrane is chiefly in the same condition as in all pneumatic canals, that is, firmly attached to the tissues about it, and only having folds at certain definite spots, at that point where the accessory fissure begins fold-like projections are produced between this fissure and the safety tube; these vary in size and form in different individuals. In the majority of cases the fold on the lateral side is more marked than that on

Fig. 378.

Fig. 378. Section of the middle third of the Human Eustachian tube. 1, 2, cartilage; 3, musc. dilatator tubæ; 4, folds of the mucous membrane under the cartilage hook; 5, small folds of mucous membrane in the accessory fissure; 6, sub-mucosa.

the medial; the opposite arrangement, however, may be observed, and just so far as these folds project, so far the safety tube is incapable of closing. A closure of the safety tube is first possible at the point where the bend of the cartilage becomes narrower, and the mucous membrane is no longer in such close union with it.

This point is found about the middle of the Eustachian tube, where the mucous membrane has a slight undulating outline, as is shown in fig. 378 The configuration of the cartilage renders it possible here for the surfaces of the mucous membrane to lie in contact, when the relaxation of the muscles allows the elasticity of the two cartilaginous plates to bring the surfaces together. When under the microscope a fissure is seen in the centre of the section, it should be distinguished from the oval or semicylindrical openings found under the hook of the cartilage in the upper third of the section.

The safety tube is very well marked in the feline race, in the Horse,

Fallow Deer, Sheep, Goat, Calf, Heifer, Rabbit, and Hare; on the other hand, it is not found in the form just described in the Apes, the Woodchuck, Dog, Marten, Hog, and Otter.

In the Sheep, Red Deer, Goat, and Calf fine folds are met with on the concavity of the cartilage, which were described by me in 1867 and 1868; they do not however extend along the whole length of the tube, but are confined to its upper portion. Many such folds are seen in the Sheep, Goat, and Calf, but in the Heifer they have united in a single projection.

The greatest projection in the Calf measures, from its base to its point,

Fig. 379.

Fig. 379. Section of the cartilaginous Eustachian tube of the Ox. 1, medial cartilaginous plate; 2, a long process directed towards the medial line; 3, hook-shaped cartilage; 4, lateral end of the cartilage; 5, musc. dilatator tubæ; 6, safety tube with the fold of the mucous membrane; 7. wide part of the Eustachian tube at the beginning of the accessory fissure; 8, accessory fissure.

0.042–0.064 mm., and in the Ox, 0.080–0.096 mm., so that from these measurements it is apparent that we are dealing only with differences of size of one and the same tissue at different ages. It is highly probable that the folds on the concavity of the cartilage serve to render it movable, and we may also assume that these never in life reach the size in which they are found after death.

Along the accessory fissure in the pharyngeal portion of the Eustachian tube, where the surfaces of the mucous membrane are in apposition during relaxation of the muscles, numerous folds are found which have been described by Huschke and F. Arnold. These are also related to the mechanism of the tube, since they are found preferably at that point where the medial cartilaginous lamella has the greatest degree of mobility. They are found with modifications in the majority of animals which have been examined,

and have reached their highest degree of development in the tube of the Woodchuck and the Otter, in which only a simple curved fissure, without safety tube, exists.

A peculiar formation is seen in the Eustachian tube of Bats and Horses, where the mucous membrane forms a lateral pocket or open-air cavity, surrounded by muscles and glands (*v.* fig. 381).

In the Bat this sac has a long rectangular shape, produced by the glands and muscles, which unite with it externally.

In the Horse the wide safety tube is separated from the accessory fissure

Fig. 380.

Fig. 380. Mucous membrane with the neighboring glands and folds from the accessory fissure of Man. 1, strongly developed folds of mucous membrane, with a fibrous layer, which encloses many nuclei, and which lies just below the epithelial layer; 2, sub-mucous fibrous layer; 3, acinous glands; 4, their excretory passages, with a transitional epithelium; 5, ciliated epithelium on the lateral wall.

by a strongly developed projection of the mucous membrane, which is continued into the air-sac. This sac reaches almost the whole length of the tube, and the air-sacs of the two Eustachian tubes reach to the medial line in front of the vertebræ and are contiguous to the base of the skull, and to the transverse processes of the first two cervical vertebræ.

The histology of the mucous membrane is as follows: its inner surface has on all sides a ciliated epithelium of several layers, which is 0.020 mm. thick. In this epithelium, both in the osseous and in the cartilaginous tube, two varieties of cells may be distinguished.

Those on the free surface stand close together, are broad on the ciliated

surface and become narrower toward the other end, which passes into the deep cell-layer. The cells of this deeper layer are broad on the basal membrane and their smaller ends are inserted between the cells of the superficial layer. The nuclei of the former are long, those of the latter rounder, smaller, and much more succulent. F. E. Schultze has described also chalice-like cells in the epithelium of the Eustachian tube, and whenever I have examined my finest sections with reference to these cells, I have found between the cylinder cells quite broad openings, at regular distances from each other, the arrangement of which nearly corresponds with what have been described and figured as chalice-like cells.

Fig. 381.

Fig. 381. Section of the Eustachian tube from Vespertilio murinus. 1, medial cartilaginous plate; 2, thin hook; 3, lateral end of the hook; 4, oval-shaped safety tube; 5, accessory fissure; 6, rectangular air-sac; 7, musc. levator veli palatini; 8, thick glandular layer; 9, excretory duct of the gland.

Next the epithelium and basal membrane is a fibrous layer containing numerous nuclei, which varies in its nature in the osseous and cartilaginous tube. The layer of connective tissue in the cartilaginous Eustachian tube alternates in thickness with the glandular layer; where the gland substance is strongly developed, as in the neighborhood of the accessory fissure, the fibrous layer diminishes; where the glands are entirely wanting, as in the safety tube, the fibrous layer is distinct. A thick entangled connective tissue of considerable consistency appears in the upper part of the osseous tube, under the lateral portion of the cartilage, and with this layer the tendinous fibres of the musc. dilatator tubæ are here and there interwoven. At this point also on the floor of the accessory fissure a thick connective tissue exists, with which the tendinous fibres of the musc. levator veli palatini are partly interwoven. It may be said that here the upper end

of the Eustachian tube, near the bone and the cartilage hook, receives a stiff frame on which the muscles can exert a very slight influence. Passing farther downwards, a distinct boundary is found between the flat tendon of the dilatator tubæ and the sub-mucous connective tissue, and deeper still a layer of fat is situated.

The mucous glands are entirely wanting in the neighborhood of the safety tube, throughout the whole length of the Eustachian tube. On the middle portion of the accessory fissure the acinous glands form a layer between the medial cartilaginous plate and the mucous membrane, and this

Fig. 382.

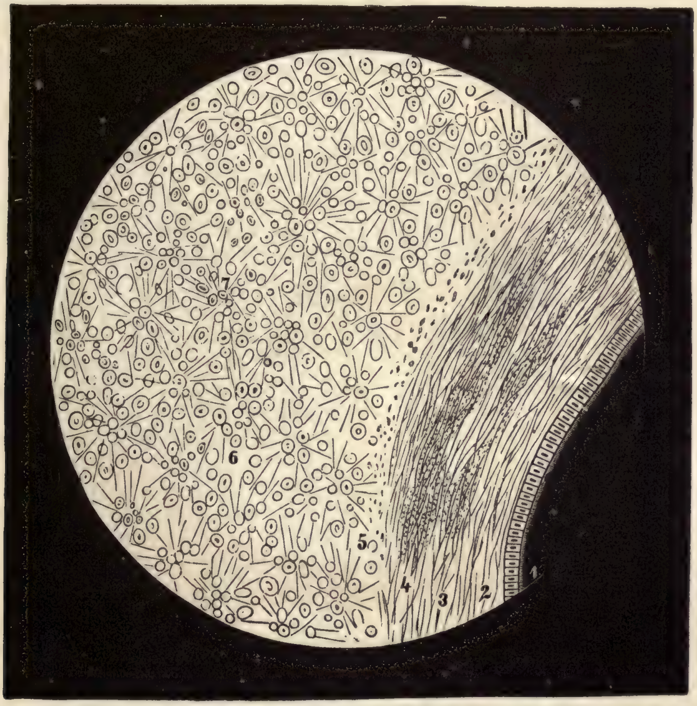

Fig. 382. The cartilage united with the mucous membrane of the safety tube. 1, ciliated epithelium; 2, sub-mucosa; 3, thick fibrous layer; 4, perichondrium; 5, cartilage cells with small oblong nuclei; 6, group of fibres with cartilage cells. $\frac{170}{1}$

becomes gradually thicker as you pass downwards. Glandular lobules are found also on the lateral side of the tube, between the dilatator tubæ and the epithelium, and reach at some points as far as the blunt end of the lateral cartilage. The mucous glands do not differ in their formation from those of the pharynx and œsophagus. The single acini by aggregation form larger ones, and their quite broad excretory passages enter the tube at different points. The epithelium of these passages is a transitional form between the epithelium of the mucous membrane and that of the glandular lobules. The round or oblong acini are so filled with wedge-shaped epithelial cells that only a small cavity is left in their centre.

In the different classes of animals the acinous mucous glands show a very great variation in size and number. In the Apes, Bats, Woodchucks, Sheep, and Goats they form a thick layer confined either to certain spots or to the whole central and medial side of the accessory fissure; in all the other animals which I have examined they appear reduced to a thin layer in the sub-mucosa. Histologically I can recognize no difference in the lobules except in their size.

4. Nerves.

In the nerves of the mucous glands of the Human Eustachian tube I have already described groups of ganglion cells. The nerve bundles, consisting of fibres with a double outline which arise from the plexus tympanicus and the plexus pharyngeus, form a coarse network which contains ganglion cells in variable numbers at those points where the bundles meet. The ganglion cells are of different sizes, and their processes unite with the primitive fibres. These ganglia correspond to those which occur in the branchlets of the plexus promontorii (E. Bischoff), and inasmuch as the nerves of the Eustachian tube are to a great extent reinforced from this very plexus, with branches which also contain sympathetic fibres, their morphological relation to the plexus tympanicus (W. Krause) can hardly be denied, although in accepting this view we do not exclude the possibility of their being functionally related to the mucous glands.

5. Vessels.

The vessels of the Eustachian tube arise from two different sources, from the vessels of the tympanum, and from those of the pharyngeal wall. The latter show nothing peculiar in their arrangement, but correspond in their relations with the capillaries of the pharynx.

The former, on the contrary, run first as large arterial branches in the direction of the tube, along both its floor and also the safety tube, and on cross-sections they are found to be confined to certain positions. Two vessels of variable size are seen in the projections of the mucous membrane which lie between the safety tube and the accessory fissure; one of them forms a capillary network on the lateral, the other on the medial side, and these networks do not anastomose with that of the third vessel, in the middle of the safety tube (*v.* Fig. 377). This third vessel forms a distinct capillary network in the sub-mucosa, and is distributed only to a definite portion of the roof of the tube.

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III.—The Membranous Labyrinth.

1. *Topography and Histology.*

Doubts, based upon experimental observations, are constantly being raised against the physiological rôle hitherto attributed to the membranous labyrinth in the function of hearing; at the present time, however, this membranous structure should be considered as an integrant part of the internal ear—as the support of the apparatus for the perception of sound. Its topographical and histological relations are found to vary in many respects in the different classes of animals. In many Invertebrates, as well as in Mollusks and Crabs, the labyrinth is represented by a bladder-shaped structure which is usually attached to the nervous centre or to one of its

Fig. 383.

Fig. 383. Membranous labyrinths of Vertebrates:—A, of Man; B, of the Calf; C, of the Pike; D, of Vultur fulvus; E, of Rana esculenta. 1, canalis semicirc. horizontalis; 2, can. s. superior; 3, can. s. posterior; 4, canal. communis; 5, ampuliform termination of the canalis s. horizontalis; 6, utriculus; 7, sacculus rotundus.

branches (in the Achetidæ and Locustidæ among Insects it occurs at the knee-joint, but in the Acrididæ, above the origin of the last pair of feet); whereas, in almost all Vertebrates we find the *membranous labyrinth*—which constitutes only a part of the acoustic apparatus—more or less completely embedded in a cartilaginous or osseous capsule, of which it repre-

sents the diminished cast. The long saccule with its ampullæ and semi-circular canals, as well as the round saccule, *lie in direct contact with the osseous or cartilaginous capsule*, and are not, as hitherto erroneously supposed, bathed on all sides by fluid (the perilymph).

These topographical relations of the labyrinth may be recognized, even during embryonic life.* Transverse sections through petrous bones, at various stages of development, show that the space within the vestibule and semicircular canals is filled with a gelatinous tissue, which first becomes firmer in consistency along the cartilaginous wall, and that the labyrinthine structures are connected with this somewhat denser fibrous layer. The vessels which become developed here traverse the gelatinous tissue in the following manner: the larger twigs, which are seen in cross-section, run in a direction that corresponds to the long axis of a semicircular canal, while the branchlets that are given off from them pursue a more transverse or oblique course. Of the two larger vessels (see Fig. 384), which are always a little separated from each other, I consider the narrower one to be an artery, and the broader one a vein. When, therefore, by reason of the retrograde metamorphosis of the gelatinous tissue, the cavities are produced, the only

Fig. 384.

Fig. 384. Transverse section of the cartilaginous and membranous semicircular canal of the Fœtus.—1, cartilaginous semicircular canal; 2, gelatinous tissue, which completely fills the space; 3, vein; 4, artery; 5, situation of the membranous semicircular canal in close proximity to the wall.

formed elements that remain of this gelatinous tissue are the periosteum and the nucleated connective tissue which surrounds the vessels that traverse the cavity.

In Adults the periosteum investing the osseous labyrinth consists of a moderately thick layer of connective tissue with which fine elastic fibres are intermingled. This connective tissue and its vessels are continuous with the connective tissue and vessels of the bone, so that separation is somewhat difficult. In the semicircular canals the inner surface of the periosteum is uneven. Its tissue is studded with pretty large nuclei, which occur more numerously and in more regular order in the neighborhood of the free surface than in the neighborhood of the bone. In specimens which have been har-

* Kölliker, in his History of Development, was the first to give a drawing of this relation in the semicircular canal of the fœtus.

dened in chromate of ammonia or chromic acid they constitute, sometimes, regular rows, so that in many respects they seem to present the character of pavement epithelium. Still a number of recent examinations, in which well-hardened specimens were used, have convinced me, I believe, that we do not really meet with any epithelium at all, but only numerous nuclei of the periosteum—a fact which Henle and Hasse have already called attention to. Henle finds the periosteum of the labyrinth of the same character as the subarachnoid, but the pigment cells are few in number. The chalky concretions contained in the periosteum, described by Kölliker and Henle, have eluded the observation of some observers, while they have been found by others in great abundance.

Fig. 385.

Fig. 385. Long and round saccule from a camera-lucida drawing. 1, utricle; 2, round saccule; 3, macula acustica; 4, ampullæ; 5, canalis communis.

In certain portions of the periosteum not only the two saccules in the vestibule, but also the membranous semicircular canals adjoin one another internally, a fact which is recognized when one attempts, with the help of the chisel, to expose the labyrinth. To gain a clear insight, however, into the mutual histological relations between the bony and membranous labyrinth it is necessary to make sections through the pars petrosa, previously deprived of its earthy constituents by chromic acid. It may be mentioned that the utricle lies more internal to the bony portion of the median vestibular wall than the round saccule; this, as Odenius has also stated, is separated from the recessus hemisphæricus by a pretty broad, loose layer of connective tissue, which surrounds the nerve fibres and the vessels traversing it.

The utricle and round saccule together embrace about two-thirds of the vestibular space. The utricle extends further in a lateral direction than

the round saccule, but neither one of them touches the foot-plate of the stapes, which constitutes the principal portion of the lateral wall of the vestibule—a feature which I described as early as the year 1866.

On the convex side of the osseous passages the membranous semicircular canals are attached to the periosteum by pretty strong bands of connective tissue, which I shall term *ligamenta labyrinthi canaliculorum et sacculorum.* Where the membranous canal lies close to the bone the periosteum is feebly developed; but where it is not adherent to the bone reinforcements of nucleated connective-tissue bundles extend from the periosteum to the outer fibrous layer of the canal, and these ligamenta labyrinthi canaliculorum represent *the most important means of holding it in place.* Sometimes there are two or more bands, which include variously formed interspaces between them.*

Fig. 386.

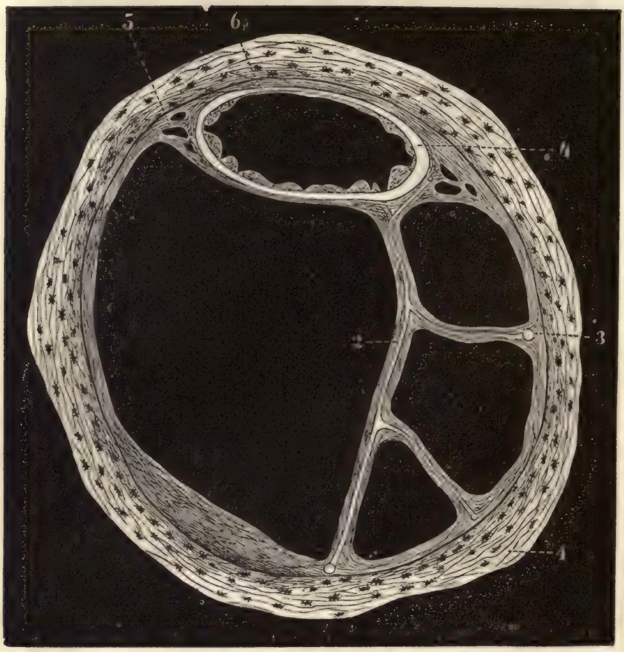

Fig. 386. Transverse section of the Human osseous and membranous semicircular canal. 1, bony wall; 2, connective-tissue bundles with the vessels enclosed in them; 3. union of the fibres with the periosteum; 4, membranous semicircular canal with its three coats; 5. ligamenta canaliculorum with its interspaces; 6, point of union between the membranous semicircular canal and the periosteum.

These interspaces look like transverse sections of small canaliculi which run in the ligaments parallel to the great membranous canal. They are perceived again in the neighborhood of the ampullæ, but I do not believe that any special morphological or physiological significance is to be attached to them. In the saccules and ampullæ, too, these ligaments, or rather stays, are feebly developed in those portions where the saccules

* *Aerztliches Intelligenzblatt*, June.

recede from the bone. Vessels are also uniformly met with in transverse sections of these ligaments.

The office of the pretty tense and finely fibrillated bundles of connective tissue in the free cavity of a semicircular canal (fig. 386), which on one side are in relation with the periosteum and on the other side with the labyrinthine wall, is to be regarded as chiefly to furnish a support for the vessels, as well as to hold in place *the free wall* of the membranous canal. These bundles usually intersect the longitudinal axis of the semicircular canal at a right angle, send accessory branches to the periosteum, and, becoming gradually larger, attach themselves firmly by their termini at the most varying points. The two saccules are attached in a very similar way, the only difference being that at those places where these bodies recede from the bone the finely fibrillated connective tissue (the *ligamenta labyrinthi sacculorum*) appears much more feebly developed.

In *Apes and other Mammals* the labyrinth, which, in general, is very thin-walled, appears to be attached precisely as in Man. As to its connection with the periosteum and the vessels with their envelopes of delicate tissue, the only difference is that the ligamenta labyrinthi canaliculorum do not seem to be so sharply defined.

In the Rat the bony canal is traversed throughout by retiform connective-tissue bands and studded with pigment cells, about one-half the cavity being occupied by the membranous canal, which is eccentric in position, so that here the relation between the size of the bony and membranous canals is entirely different from what we have observed in Man.

Fig. 387.

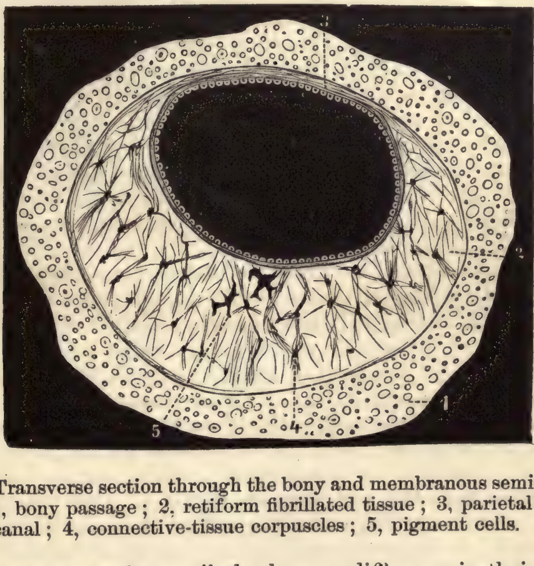

Fig 387. Transverse section through the bony and membranous semicircular canals of the Rat. 1, bony passage ; 2, retiform fibrillated tissue ; 3, parietal lamina of the membranous canal ; 4, connective-tissue corpuscles ; 5, pigment cells.

The two saccules in the vestibule show no difference in their mode of attachment. In the bony semicircular canals of *Birds*, also, the position of the utricle, both according to Hasse's and my own observations, is eccentric. The membranous ampullæ, on the other hand, appear in some respects as casts of the bony, so that they touch the periosteum of the bone at their entire peri-

phery. The membranous passages are contiguous to the periosteum, at points corresponding to the convex side of the bony passages; but they do not seem to be buried in the periosteum as in Man.

Their free wall is united with the periosteum by a fine network, and we may convince ourselves that both in the Rat, as also especially in Birds, Fishes, and the short-tailed Batrachia, the space which borders the free surface of the membranous canals and the utricle is not enveloped by any tunica serosa bearing epithelium.

Fig. 388.

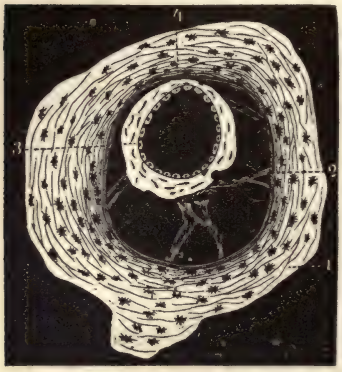

Fig. 388. Transverse section of the bony and membranous semicircular canals in a Goose. 1, bony upper canal; 2, fibrillæ uniting periosteum and membranous canal; 3, membranous canal with epithelium on the under surface; 4, attachment of the thin portion of the membranous canal to the periosteum.

In *Fishes*, too, the membranous semicircular canal is attached to the firm canal wall. The proportionately wide cartilaginous or bony passage is here partly filled by a network of broad fibrous bands which surround a system of interspaces filled with mucus.

The remaining space contains the membranous passage, which adheres loosely to the wall, and also a delicate network of fibres that is not essentially different from the above-mentioned mucoid tissue in the semicircular canal of the Human fœtus and Frog.

Hasse in his first articles claimed for the *Frog* that markings as of epithelium existed on the external surface of the membranous semicircular canal. Sections, however, made through the bony and membranous labyrinth, and especially through the bony semicircular canal, exhibit histological relations which do not sustain the theory of a tunica serosa. For, in examining successful sections we observe that anastomosing connective-tissue corpuscles—called in the Human embryo mucoid tissue—entirely fill the canal. Whether the same condition is seen at all ages in this animal I must leave undecided at present, for my data, thus far, relate only to Frogs examined at the end of the winter.

In the gelatinous tissue of the Frog there are numerous large pigment cells, of which some attach themselves internally to the outer side of the membranous canal. There is a still more abundant deposit of pigment cells in the neighborhood of the utricle and the stone sac in the vestibule, so that the points where nerve bundles and vessels penetrate the utricular wall are somewhat difficult to discover. It is to be observed in regard to the distance of the Frog's membranous labyrinth from the bony wall that the utricle, the stone sac, ampullæ, and the commencements of the membranous portions lie pretty close to the fixed capsule, while, on the other hand, it cannot be denied that the membranous canals, as they recede from the vestibulum, separate also more from the wall of the bony labyrinth, so that they appear to be entirely enveloped in the nucleated fibrillary connective tissue.

For those who are inclined to look upon this arrangement as artificial there is this additional fact to be taken into consideration, viz., that the attachment of the entire membranous labyrinth to the periosteum in the Frog is by no means so intimate as in Birds, Mammals, and Man, a fact which

perhaps can be regarded as dependent on the grade of retrograde metamorphosis of the mucoid tissue.

2. *Labyrinthine Wall.*

The histology of the labyrinthine wall is most advantageously studied on cross-sections. The thickness of the semicircular canal, which on cross-sections appears to be oval, is not uniform (fig. 389). In Man the thickness of the canal bordering on the bone, exclusive of periosteum, measures 0.016 millim., the free wall measures 0.028 millim., and that portion which is attached by the ligamenta labyrinthi canaliculorum has a diameter of from 0.060 to 0.080 millim.

We can differentiate four layers of tissues: first, a layer of connective tissue; second, a hyaline tunica propria; third, papilliform (villiform) processes; fourth, epithelium.

The *external fibrous layer*, which for the most part encircles the canals, represents a connective-tissue substance, studded with numerous nuclei, and does not appear to be essentially different in its structure either from the

Fig. 389.

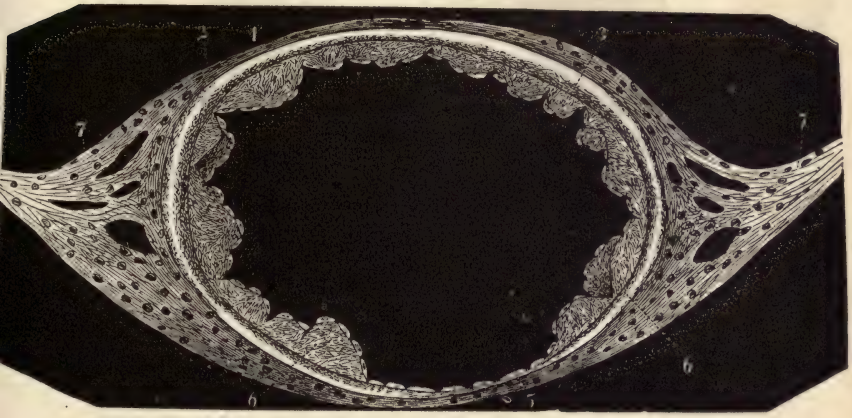

Fig. 389. Transverse section through the membranous semicircular canal in Man. 1, free wall with the fibrous layer and connective-tissue corpuscles; 2, tunica propria; 3, papillæ with their epithelium; 5, part of the canal wall showing no papillæ, and having a very thin tunica propria; 6, increased development of the papillæ on the border of the non-papillary portion; 7, ligamenta labyrinthi canaliculorum.

ligaments described above or from the periosteum. At the point where the canaliculus touches the periosteum, the external fibrillar coat constitutes an extremely thin layer, but becomes stouter on the free wall, and reaches the highest grade of development where it coalesces with the ligamenta labyrinthi canaliculorum. The arrangement of the large and usually rounded nuclei that are embedded on the outer surface of the free side of the canal is such that we have quite the appearance of an epithelial layer. The nuclei, however, are similarly disposed in the labyrinthine ligaments and on the periosteal side; finally, well-stained preparations demonstrate that the external surface of the membranous passage has no pavement epithelium.*

* According to Schwalbe and F. E. Weber the space between the membranous and bony labyrinth, which is filled with perilymph, is a lymph space, for masses injected from the arachnoidal cavity through the porus acusticus penetrate into it.

In examining the semicircular canals as a whole after taking them from their bed with their periosteum and ligaments, we perceive, in the neighborhood of the vessels, another network of fibres, whose significance I was formerly doubtful of. Pretty broad bands of fibres, pale in appearance, form retiform connections with one another. At the commissures, where they are much broader, and their fibrillar character is most defined, large cells with nuclei are embedded in varying numbers. At the first glance this network

Fig. 390.

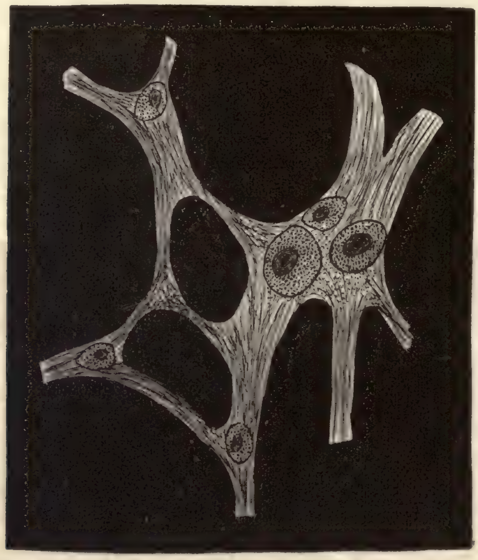

Fig. 390. Network of fibres containing embedded cells from the periphery of the vessels in the semicircular canals of Man.

has quite the appearance of *nerves* with embedded ganglionic cells (fig. 390). Whether we really have to do with nerves or a new sort of connective tissue I was unable to bring to a final decision before the conclusion of this article. It is hardly necessary to add, that it would be of the greatest interest if this observation proves to be a re-discovery of the nerves belonging to the membranous semicircular canals and whose existence has hitherto been doubted. The fibrous layer forms a delicate coating over the saccules, excepting only at those points where the nerves enter the bony wall. The saccules do not actually adjoin the bony wall so closely at this point (the utricle more intimately than the round saccule), but they are separated from it by a broad-meshed connective tissue which embraces the vessels and nerves.

The second investing coat, too, the hyaline *tunica propria*, varies in thickness; it is very thin when seen in section, at the point where it is contiguous to the membranous canal, but along the free wall it is somewhat stouter, and attains a considerable volume about the area of attachment of the labyrinthine ligaments. The fresh preparation represents a hyaline substance which seems neither to be sharply defined outwardly, towards the fibrous coat, nor inwardly, towards the papillæ. By employing coloring materials and other reagents a granular, delicately striated character is

given to the tunica propria. This same substance is also observed on the utricle, but here forms a very thin uniform layer.

The *papilliform* * *prominences* on the inner surface of the tunica propria I must hold as *normal structures belonging to adult Man.*

They occur so uniformly that I should be inclined to regard their absence as pathological rather than exceptional. They seem to be limited to certain portions of the canal wall, and for this reason I have already alluded to a *papillar* and a *non-papillar* part of the wall. In Adults we observe them as "hyaline spheroids" of various forms and dimensions in the membranous canals; on transverse section they are recognized as prominences. They rest upon the tunica propria with a broad base, and project into the lumen of the canal as little mound-like, club-shaped, or conical processes. In the direction of the tunica propria the papillæ are not sharply defined, and they must really be regarded as integral parts of the membrane, for when they exist they arise from it and are in structure entirely identical with it. †

In the embryo and even in new-born Children the papillæ are still entirely wanting, but appear subsequently on those portions of the inner canal-wall where the labyrinthine ligaments attach themselves externally. The thin portion adjoining the bone of the membranous semicircular canal is entirely free from papillæ throughout its greatest extent, and I have never seen in it the slightest vestige of them, notwithstanding the tunica propria is present here, though only as a very thin layer (*vide* fig. 389). On both sides, however, the mound-like prominences begin, increase gradually in size, and finally to the right and left become stouter (turn to the diagram), diminishing again in height at the free labyrinthine wall. At the latter point they often raise themselves very little above the free surface, so that with low powers they appear to be absent. Their entire inner surface, both in the depressions between the papillæ as also on their tops, is invested by a single layer of pavement epithelium, which, both in surface and profile sections, can be pretty easily brought into view by employing the various means of investigation at our command. Since, however, these epithelial cells are pretty easily detached, and the smallest papilla often bears only from three to five of them (*vide* fig. 391), the nuclei of the cells cannot always be seen in profile in cross sections, a fact which aided very materially in leading to a denial of the existence of epithelium on the top of the papillæ (Lucae). The cells in the papillæ and in their neighborhood appear of irregular form, and in surface views it is quite possible to follow those that have imbibed nitrate of silver over all the points of inequality. Since the formations we are discussing do not appear until after birth, it is probable that, during their development, they in a simple mechanical way spread out the epithelia which were originally arranged at regular intervals. The same must also be claimed for many of the peculiar forms of epithelium which Eberth has brought to our notice, and for the lung-vesicles, as if it be true that in Adults they bear epithelium.

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* In place of the term "villiform," which I have formerly employed, I propose the word here introduced, since the formations under discussion have more similarity with papillæ than with villi. Hasse has ventured the supposition that I have regarded the striæ to be seen through the tissue as papillæ, or rather villi, a supposition which forces me to conclude that Hasse had not studied these structures in Adults, for it is a most simple matter to obtain a sectional view of the papillæ, and any misconception is impossible.

† Whether the papillæ are identical with the "great globes" described by Pappenheim, cannot be determined from his obscure statements. (See pages 43 and 44 of his *Gewebelehre des Gehörorganes.*)

Though there are individual variations in regard to the papillæ, yet I have never found them entirely wanting. At some distance from the thin wall, at points corresponding to the attachments of the canal ligaments, they are never absent; sometimes, however, on the free side of the canal they are only feebly represented. In the saccules, and near where the semicircular canals open into the utricle, they are not found. Still, on several occasions I have seen isolated papillæ at the expanded orifices of the horizontal membranous passage.

Fig. 391.

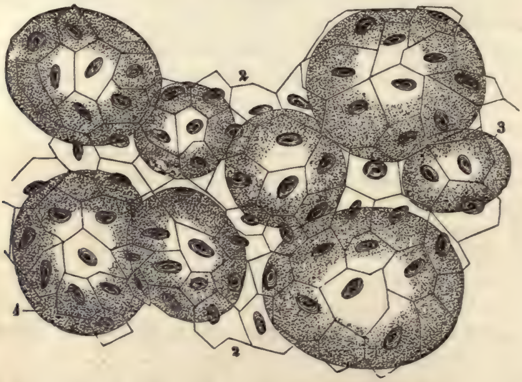

Fig. 391. Surface view of the papillæ in the horizontal membranous semicircular canal. 1, 2, 3, papilliform formations with the epithelium (nitrate of silver preparation.)

These formations peculiar to adult Man have been regarded as pathological in their nature (Voltolini, Lucae).

Lucae asserted that they were not present in new-born Children, and, from the fact of their having no epithelium and showing a reaction with iodine, would place them among the group of amyloid bodies. On the other hand, passing over the first point, which is irrelevant, I reply that, first, I have never entirely failed to see papillæ in the semicircular canals of Adults, even though each one was developed in a different degree;* second, that by means of suitable reagents epithelium is demonstrated, and though they show the well-known iodine reaction, the same is true of the tunica propria and many other tissues, in which amylum has yet to be discovered. It will not certainly be urged that the rounded forms which the papillæ show when torn by artificial means are any proof of their amyloid nature. I have convinced myself most conclusively in very fine transverse sections of the membranous semicircular canals that the papillæ are only to be regarded as parts of the tunica propria. The border line which appears in transverse sections between the membranes mentioned above and the papillæ (*vide* fig. 389) depends merely on the thickness of

* If we examine the membranous labyrinths in the cadavers of thirty Adults, taken at random, as they are brought into the anatomical room, and taking no account of the diseases to which they have been subject, we shall find in about 28 the papilliform prominences and in 2 none at all. Now this numerical consideration, excluding others already mentioned, would be a sufficient reason for not regarding them as pathological formations.

the cut. In very fine sections high powers fail to discover to us any contours between both layers. When it can be claimed that the membranous canals secrete the endolymph, then the papillæ, entirely apart from other physiological considerations, appear at once as formations which cause a considerable increase of surface.

In Mammals the parietes of the membranous labyrinth are considerably thinner than in Man. The thickness of the membranous semicircular canal varies only in slight degree and its mucous membrane is free from papillæ.

The wall of the membranous labyrinth of Birds varies in thickness in the utricle, the ampullæ, and more especially in the semicircular canals. The semicircular canal which appears oval in transverse section is very thin at the point where it adjoins the osseous wall, and increases gradually in thickness as it recedes from this point. The thinnest part has a diameter of 0.020 millim. and the thickest of 0.080 millim. I cannot agree with

Fig. 392.

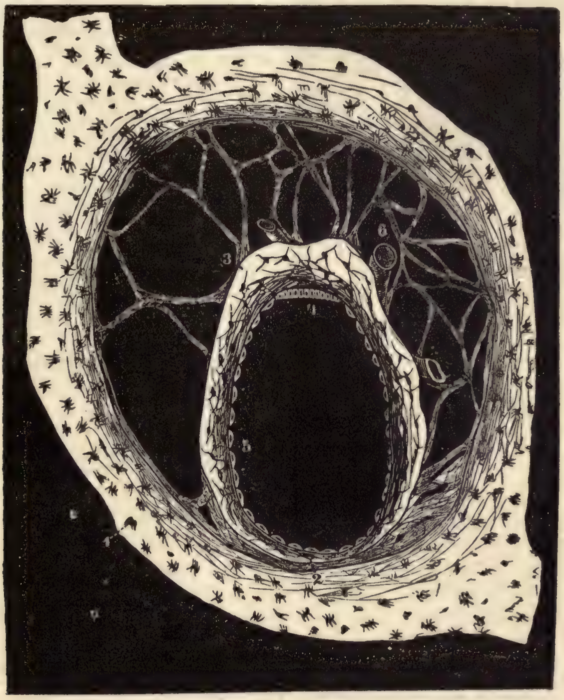

Fig. 392. **Transverse section of the sagittal semicircular canal in a Pigeon.**
1, bony semicircular canal; 2, thin section of the wall united with the periosteum; 3, thicker portion of the wall with a groove for an artery; 4, epithelium, to be distinguished from flattened epithelium; 5, flattened epithelium; 6, retiform framework of fibres between the periosteum and outer surface of the membranous semicircular canal. $\frac{170}{1}$.

Hasse that the thickness of the wall varies within certain limits, and that no rule can be laid down as to a greater or less thickness in certain parts. My examinations have convinced me that the thin canal wall is entirely limited to the point where it rests on the periosteum, and the thick wall, which

externally has a sort of groove for the reception of the larger vascular branches, is on the side of the canal distant from the bone.

There is a fibrous layer where the connecting substance in the bony canal unites with the outer surface.

The stout tunica propria which forms the wall, in connection with the epithelium on the basal border of the inner surface, has already been named "*labyrinth cartilage*" in Birds, Fishes, and Reptiles. The excellent works of Leydig, Deiters, and Hasse contain the histology of the canal wall illustrated by plates.

In a structureless basis substance, which only after treatment with chromic acid becomes finely granular, there are embedded numerous small nuclei, long or quadrangular in form, with processes. The majority of the outrunners from the connective-tissue corpuscles surround the canal chiefly in a circular manner, others penetrate the thick portion of the canal in a direction from without inward (fig. 393). The coarse vascular nets which surround the membranous canals rest in part also in the cartilaginous substance, without, however, reaching the epithelial layer. This latter, resting on a basal membrane, invests the inner surface as a regular pavement epithelium. A larger variety of epithelium, limited to a small space, appears on the thick side of the canal; here it appears somewhat as if we encounter those cylindrical cells of the utricle and of the ampullæ which form a narrow belt opposite the nerve epithelium, and were very accurately described by Hasse under the name of "Roof-cells" (Dachzellen).

Fig. 393.

Fig. 393. Sagittal semicircular canal of the Pigeon. 1, groove on the thick portion of the canal for the reception of a vessel; 2, thinner parietal section; 3, labyrinth cartilage traversed by larger vessels; 4, flattened epithelium. $\frac{170}{1}$.

The comparatively thick-walled canals of Fishes * vary as to the thickness and shape of the lumen in different families. In the Pike (fig. 394) the canal is triangular on transverse section, with a base corresponding to the free thick wall, and two sides which, arching over, meet in a thinner portion. That portion which adjoins the bony or cartilaginous canal-wall is here, too, the thinnest.

This has a diameter of 0.080 millim., while the thick portion measures from 0.120 to 0.160 millim. It consists of a firm hyaline basis substance, studded with very numerous stellate connective-tissue corpuscles, which, through the mutual attachments of the somewhat granular outrunners, represent a coarse network; in the Pike this net, on closer examination, shows an arrangement as seen in fig. 394. On the thin wall the fibres invest the lumen of the canal; at the two thickest places they appear as bands, which in transverse direction traverse the wall from without inwardly. There is no lamina of connective tissue on the outer side of the canal. On the basal border of the inner surface there is a flattened epithelium, which is formed

* My researches were confined to the Perch, Carp, Salmon, and Pike families.

of pretty large cells with stout nuclei which, seen in profile, have a fusiform appearance. In the Pike this forms a much broader border on the thick side of the canal than in the other places, and here there appears another variety of cylindrical epithelium. In no kind of animal do the epithelial cells detach themselves so easily from the basal membrane as in the Fishes, where the entire layer of investing cells may shrink, and attach itself at any point of the cartilaginous wall, giving the appearance on cross-section of a small tube.

Fig. 394.

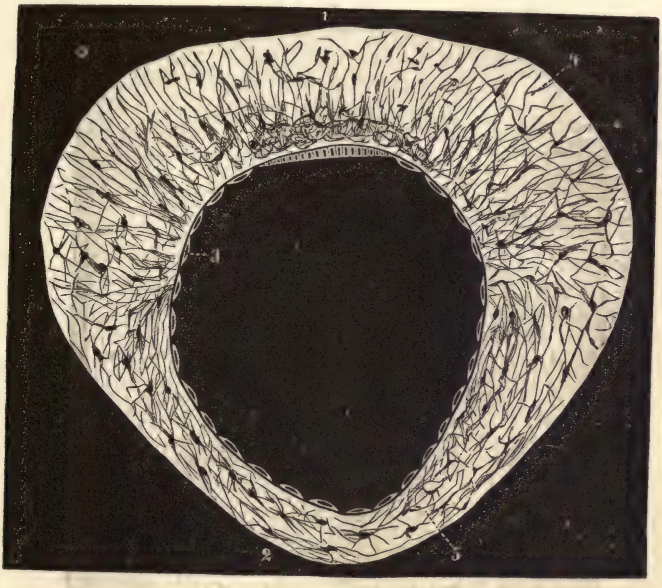

Fig. 394. Transverse section through the membranous labyrinth of the Esox lucius. 1, thick portion of the semicircular canal; 2, thinner parietal portion of the semicircular canals; 3, flattened epithelium, which assumes a cylindrical form at the thick portion of the canal wall; 4, labyrinthine cartilage with radiating fibres and connective-tissue corpuscles; 5, circular fibres with connective-tissue corpuscles.

In the year 1844 A. Ecker described ciliated epithelium in the semicircular canal of Petromyzon marinus. These cells, as H. Reich, a student of Ecker's, in the year 1857 claimed for Ammocœtes, belong only to the crista acustica or macula acustica, and not to the canals.

I have observed in the membranous passages of Salmo hucho a curious formation, standing apart by itself (fig. 395). It will be seen in the accompanying diagram that in this fish the walls and lumen of the canal differ in many respects from those of the Pike. The external side of the canal wall is uneven, its thick portion has an irregular outline, owing to a groove which exists externally, and in structure the hyaline basis substance preponderates greatly over the connective-tissue corpuscles.

In the thick portion of the wall there are two rows of cells, each of which is about an equal distance from its neighbor, and these two rows, like two walls with a furrow between them, project pretty far into the canal (fig. 395). They are to be met with throughout the entire length of the canal, and are unaltered in character, except that they are lower as they approach the utricle.

Under the epithelial cells, especially at their border, very delicate pale fibres appear, which are invested at their origin by a protoplasm, divide dichotomously, and are connected with round or oval cells, which rest on them like grapes on their stems. The entire row produced in this way floats partially in the endolymph of the semicircular canal. In surface views it is observed that both rows of cells extend towards one another in a uniform manner, bridging over the furrow, as it were. I should merely

Fig. 395.

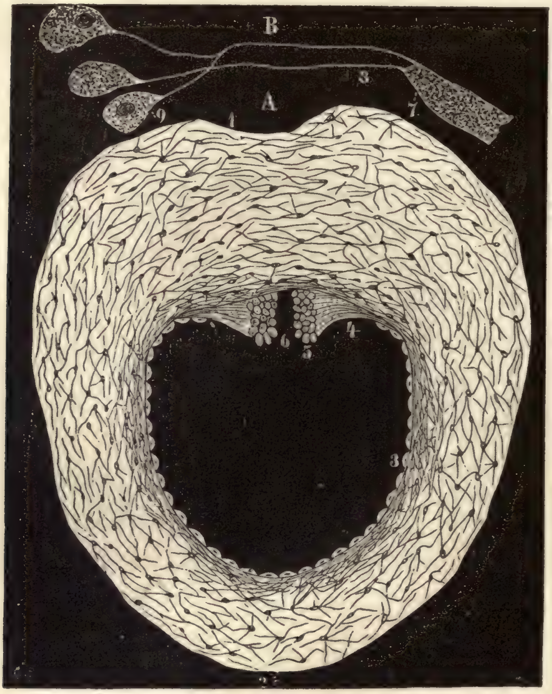

Fig. 395. *A.* **Transverse section through the membranous semicircular canal of the Salmo hucho. 1, thick portion of the canal wall, with a groove on the outer side; 2, thinner parietal portion; 3, flattened epithelium; 4, Fine fibres with the (5) row of cells; 6, furrows between the two rows of cells; *B*, highly magnified fibres and isolated cells; 7, protoplasm in which the (8) fibres appear; 9, cells in oonnection with subdividing fibres.**

like to venture the supposition that both rows are not gradually connected by their pedicles, but the cells simply touch and adhere to one another. Though on transverse section this formation presents the appearance of a complete canal, yet if we attempt to move it mechanically under the microscope, we observe that though the cells rise and fall, the rows do not cleave apart. The furrow between these walls appears to have no epithelium. I do not believe that we have before us a terminal nerve apparatus, since the branches of the auditory nerve do not pass over the border of the ampullæ, nor have I ever seen any primitive nerve fibres externally on the canal wall. It is possible that the two walls and the furrow enclosed by it have some sort of connection with the undulations of the endolymph.

Among the Batrachia I have only examined the labyrinth of the Frog. The membranous semicircular passages are almost circular on transverse section, and the wall at all points is pretty uniformly thick. Its diameter amounts on the average to 0.040 millim. A very few oval connective-tissue corpuscles are embedded in the whitish hyaline basis substance. On the outer surface there are pale fibres which penetrate transversely about half way through the wall. Since this striation appears similarly in all sections, I cannot regard it as due merely to accidental foldings. A large-celled pavement epithelium invests the inner surface.

Fig. 396.

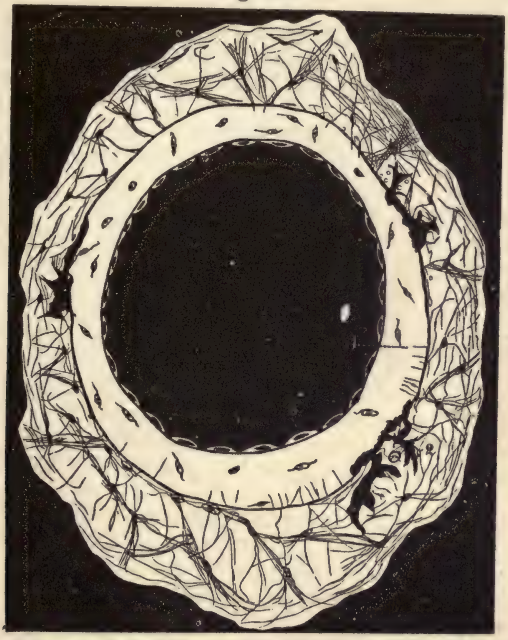

Fig. 396. Transverse section of the semicircular canal of Rana temporaria.
1, cartilage with occasional connective-tissue corpuscles; 2, network of fibres with connective-tissue corpuscles, and pigment, and cells; 3, flattened epithelium.

3. *The Vessels of the Membranous Labyrinth.*

The vascular supply for the saccules, the membranous semicircular canals, and the periosteum of the labyrinth varies according to special locality; while a rich and close network of vessels exists at the points where the nerves enter the saccules and ampullæ, the membranous canals are invested by a coarse plexus formed of long loops.

The largest arteries accompany the branches of the vestibular nerves to the wall of the round and long saccule, and form at first stout, coarse networks, corresponding to the macula and crista acustica in the loosely knit extensive connective-tissue layer, between the bony wall and that portion of the saccule-wall which bears the macula acustica. Arrived at the saccule-wall, the capillaries are finer, and form towards the periphery of the macula numerous loops, without, however, entering the tunica propria. In Birds and Fishes large capillary loops traverse the tunica propria, reaching as far as to the basal border.

In Man fine capillaries extend beyond the border of the macula acustica, and are distributed in the outer fibrous layer of the nerveless saccule wall.

Extending outwards from the vestibule, large arterial branches reach into the bony semicircular canals and pursue a course in their centre corresponding more or less to the curve of the semicircular canal. All the vessels are invested and stayed by a comparatively thick nucleated connective-tissue envelope, which remains as the residue of the fœtal mucoid tissue, to hold these vessels in place. The more delicate, tolerably thin-walled vessels given off from the larger ones in the centre of the bony canal are distributed both to the periosteum, and also to the free wall of the membranous canal and the ligamenta labyrinthi canaliculorum; from this point they return as veins embraced in their proper connective-tissue fibres. In the bony canals the arteries and veins do not lie near one another, and they are often difficult to separate from one another and from the thick-walled capillaries (fig. 384).

In the direction of the vestibule the two vessels approach nearer one another; whether, however, from here on they follow the course of the branches originating from the arteria auditiva interna, is still unsettled.

In transverse sections through the aquæductus vestibuli evidence can be obtained that near the serous passage there are stout vessels, which in external appearance appear to be veins, and have heretofore been described by Hyrtl as veins of the vestibule.

4. *Nerves and Epithelium in the Ampullæ and Saccules.*

In animals, wherever the fibres of the auditory nerve are distributed in the saccules and ampullæ, the inner surface always exhibits a peculiar epithelium, usually of a yellow color, and armed with fine hairs, and one might naturally infer, that, being found together, they should also be classed together.

In studying the topographical and histological relations of the nerves and their relations to the epithelium of the ampullæ and saccules it may be well to employ fresh objects, as well as those that have been deprived of the salts of lime and hardened in chromic acid. Sections should then be made in different directions, and these can then, if desirable, be stained and teased to pieces.*

Since the time that Scarpa and E. H. Weber had called attention to the mound-shaped prominence on the ampullæ (called by Scarpa " septum "), Steiffensand, in the year 1835, made a more thorough study of it in Fishes, Reptiles, Birds, Mammals, and Man, and has shown that the prominence, which varies in its form in the different animals, was produced by a curious wrinkling and thickening of the tunica propria of the ampullar wall. M. Schultze certainly applied more correct names to the septa; viz.: cristæ acusticæ in the ampullæ, and maculæ acusticæ in the saccules. In most animals, every branch of the nervus vestibuli which reaches the ampulla consists of two flattened subdividing bundles. They are connected with the ganglionic cells (Leydig, Hasse), and entering the furrow, to be seen externally, traverse in almost a linear direction the tunica propria to the epithelium of the crista acustica.

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* The staining method where the object is under the eye of the observer I find especially useful. In employing it I took cross-sections of the ampulla, including the nerves, placed them upon the object-slide, treated them with osmic acid, and observed the reaction as it gradually became apparent in the nerves and epithelium.

At this point the crista has a double or even triple size, and is marked on the inner side by a structureless basal border. It is not, however, alone in furnishing support for nerves; the lower portions of the walls of the ampullæ, rising laterally more or less at right angles to it, which Steiffensand has termed plana semilunaria, receive fine nerve fibres beneath their epithelium (fig. 397).

Fig. 397.

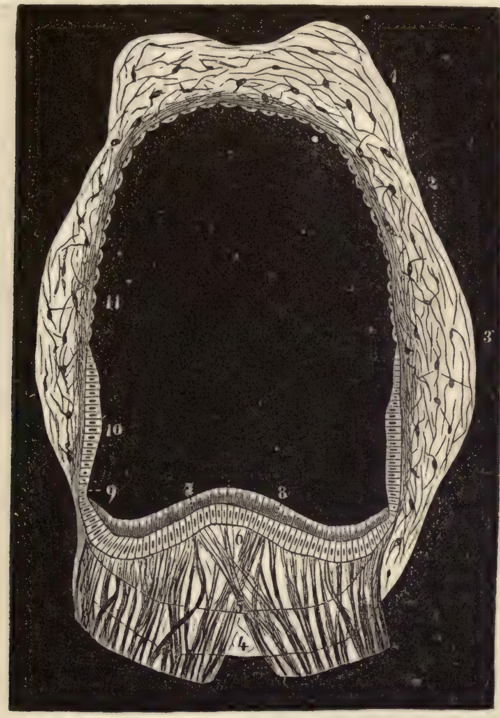

Fig. 397. Transverse section through the ampulla of the Pike. 1, roof of the ampulla; 2, thin portion of the lateral wall; 3, thickened portion of the lateral wall; 4, 5, 6, floor of the ampullæ with nerves; 7, epithelium of the nerves; 8, auditory hairs; 9, transition point between the floor of the ampulla, and 10, planum semilunare; 11, flattened epithelium.

While the primitive nerve fibres are traversing the tunica propria they near one another, and become exceedingly delicate in the neighborhood of the crista, losing their double contour. In the ampullæ of Fishes which have been treated with osmic acid it is not difficult to satisfy one's self conclusively that a pale narrow fibre, the direct continuation of a primitive fibre (as it was first claimed by Reich and M. Schultze), actually passes over the basal border of the ampullar ridge, having made no connection with ganglia, and then breaks up into a large number of finer filaments. It is so common to observe these unvarying forms in fresh and stained preparations, that there is certainly no good ground for claiming that they are artificially produced by tearing. Hartmann has been at the trouble to furnish proof that in Fishes the nervous fibrils in the crista acustica bend as it were

in loops. This statement has already been rejected by Henle, and can be very easily disproved in thin sections of stained preparations. Hartmann's conclusion that the medulla is mechanically pressed through the basal border, and thus may look very much like a divided axis-cylinder, cannot be correct when pressure is avoided; moreover it must be admitted that openings exist in the basal border, which give to the nerve-medulla the peculiar forms in question.

Fig. 398.

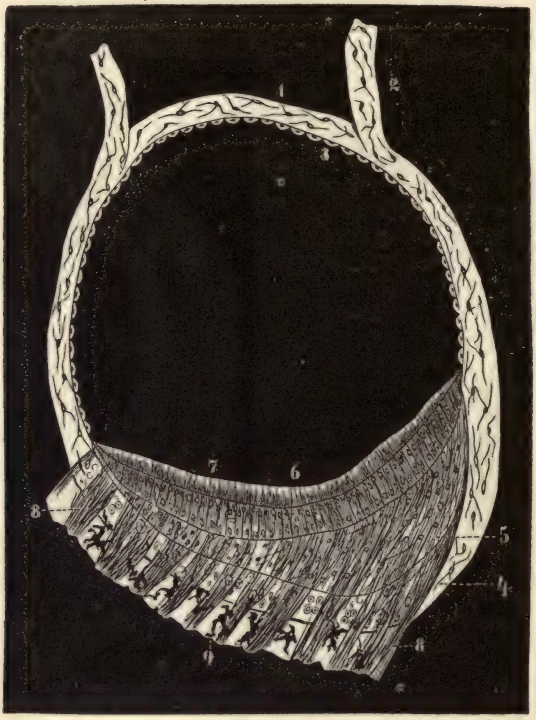

Fig. 398. Transverse section through the ampulla of Rana esculenta. 1, roof of the ampulla; 2, semicircular canal; 3, epithelium on the roof of the ampulla; 4, thickened wall of the ampulla. Nerves associated with cells; 6, 7, epithelium with the auditory ciliæ; 8, bundles of nerves; 9, pigment.

Finally, M. Schultze, F. E. Schultze, Odenius, Kölliker, Deiters, Hensen, Henle, and Hasse have expressed themselves unanimously to the effect that the pale fibres, as continuations of the doubly contoured nerve fibres, enter the epithelium.*

According to M. Schultze and Odenius, it is only the pale axis cylinders that enter the epithelium; Hasse and von Grimm claim, in addition, that the delicate sheaths enter at the same time. In Fishes a comparison of the axis cylinders of the ampullar nerves, which are readily isolated by osmic acid, with the fibres which enter the epithelium, reveals no histological

* Though Henle regards the statements of Hartmann as directly disproved, the latter states that the nerve fibres end in fine points at the basal membrane, p. 777. Henle does not feel himself entitled to oppose positive statements as to the entrance of the nerve fibres into the epithelium.

difference, even when high powers are used. As to the dichotomous division of the pale fibres, I believe that I have seen it in Frogs and Fishes even before passing over the basal border; multiple division, however, never takes place until the fibre has passed the basal border.

The layer of nerve-epithelium at the top of the ampullar wall, which appears smooth in some instances, as in Man, Mammals, and Birds, and wrinkled in others, as in many Fishes, has a varying thickness corresponding to different animals. In Birds it measures 0.016 millim. and in Cyprinoids 0.080 millim. In Mammals and in Man the thickness is intermediate between that of Birds and Fishes. The layer of nerve epithelium which rests upon the basal border is soft, loose, and nu-

Fig. 399.

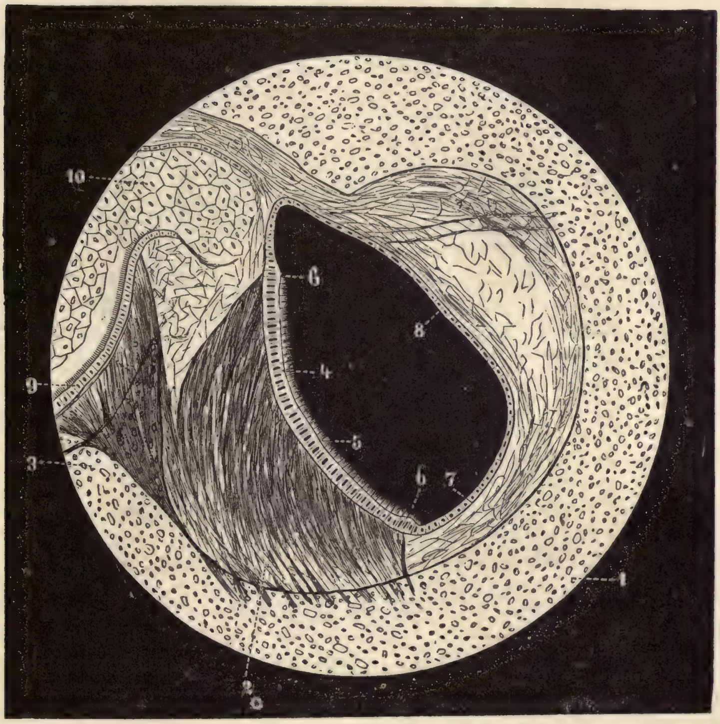

Fig. 399. Horizontal transverse section through the vestibule and round saccule of the Human fœtus. 1, cartilage; 2, nerves on the median wall of the vestibule; 3, crista vestibuli; 4, nerve-epithelium in the sacculus rotundus; 5, auditory hairs; 6, transition from nerve-epithelium into (7) the shorter columnar variety; 8, lateral wall of the round saccule; 9, utricle with the nerve-epithelium; 10, flattened epithelium of the utricle.

cleated. It appears to be thickest in the centre, and is defined on the free border by a sharply drawn line, giving an appearance similar to the limitans externa in the Human eye, and in this the stiff hairs are placed. In the Cyprinoids Lang has already described an especial layer of cells, which sometimes I have been able to recognize very distinctly. This represents a border on the inner side of the epithelial layer, and upon it the auditory hairs

arrange themselves. The cavities in the epithelium described and pictured by Lang I regard as accidental formations. In the planum semilunare of Fishes the nerve-epithelium becomes gradually broader as it extends upwards, then it becomes narrower again, and when seen in cross-section tapers down to a pointed extremity, on which the pavement cells of the upper portion of the ampulla arrange themselves; where, too, the crista acustica passes over into the planum semilunare a layer of shorter epithelium appears (fig. 397). The crista cruciata of the ampulla in Birds, which rises very abruptly towards the intermediate space, is invested throughout by a nerve-epithelium of no great thickness. In the nerve saccules the layer of nerve-epithelium is not so thick in the average as in the ampullæ.

The transition of this variety into the contiguous cylindrical epithelium is gradual here, and in the round saccule the cells are never so short as in the membranous canals, not even in those places which have no nerves; they do not appear here as purely flattened, but as transitional epithelial cells.

If we tease apart the epithelial border in Man, Mammals, and Fishes, several forms of cells are to be observed in it. First of all, we observe long columnar cells of pretty regular thickness, with a large nucleus at the central end. One end of these cells is broad, the other terminates as a truncated cone. In Frogs and Fishes they have a yellow color. These columnar cells, of which Leydig first furnished a detailed description in the Eel, Reich in the Petromyzon marinus, and M. Schultze in the Ray and Dog-fish, skirt the entire inner surface of the epithelial border, where no especial layer of cells exists. Now in the Cyprinoids, adjoining closely the inner surface, there are short, uniformly thick, bright cylinders, containing a strongly refracting nucleus, and closely applied together, which at the central margin of the auditory hairs exhibit a bright pale border. No outrunners are observed in them, and if they were not seen in situ, they might easily, from observations made of single ones, be regarded as simple cylinders from the region of the planum semilunare.

Those forms of epithelium truncated at both ends, which are present in the nerve-epithelium, seem to be only those supporting-cells (*stutzzellen*) between which the ends of the fibre-cells pass.

These spindle, fibre, or rod cells exist in much greater numbers than the columnar cells. These are the bottle-shaped or fibre-cells which M. Schultze first, and then Odenius, Kölliker, Henle, and Hasse have described with great unanimity. They show a spindle-shaped form, and have one outrunner directed towards the centre, and a little rod-shaped protuberance towards the periphery. Their pale appearance in the fresh condition makes them easily distinguishable from the other cells, but only their reaction with osmic acid appears to deserve special attention. Taking a transverse section through the ampullæ in the Cyprinoids, and observing it with the microscope after the addition of osmic acid, one perceives after a while that in proportion as the nerves color themselves dark the epithelial border with the auditory hairs also takes on a brown color, though less quickly. Finally, next the inner portion of the epithelial layer darker stripes appear, which can be traced as far as the surface. These dark striæ of unequal thickness are placed at regular intervals from one another. Finally, if we allow the epithelial border to remain a longer time in osmic acid the single cells can be isolated; and then it is apparent that in the spindle-shaped fibre-cells a black-colored stripe is to be seen, which I feel myself entitled to claim is included within the interior of the cell.

This appears as the continuation of the long fibrilla, and is connected with the nucleus of the cell; that is to say, the cell nucleus appears just as darkly colored as the thread itself. In the direction of the peripheral end the scarcely measurable thread extends, and in cells that are still provided with the residue of the auditory hairs it seems quite as if there was no lack of continuity between the dark stria in the interior of the spindle-cell and the auditory hairs. This I have often observed in the ampulla of the Cyprinoids,

Fig. 400.

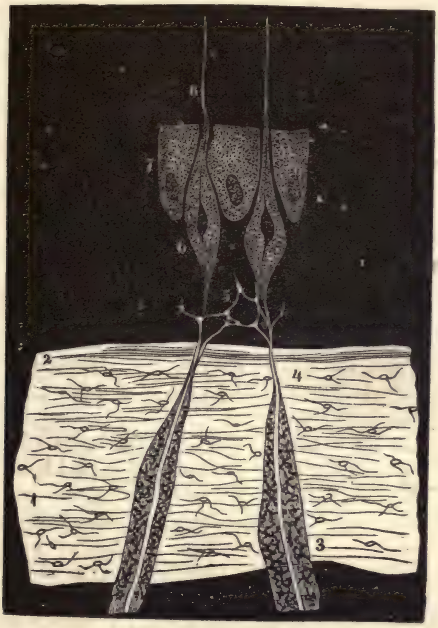

Fig. 400. Diagram showing the nerve-termination. 1, cartilage of the ampullar wall; 2, structureless ampullar wall; 3, doubly-contoured nerve-fibres; 4, axis cylinder passing through the basal border; 5, retiform connection of the fine nerve-fibres with nuclei; 6, spindle-cells with nuclei, and the dark thread in the interior; 7. supporting-cells; 8, auditory cilia.

and the reaction which takes place in the spindle-cells after employing the above-mentioned acid justifies also the supposition that nerve-forn ations exist here. In fact, these observations harmonize with the statements which recently were recognized in the ampulla by Von Grimm.*

Von Grimm, by employing osmic acid, has further seen the black coloring in the spindle-cells of the Cat. Sometimes in the simple columnar cells a dark coloring of the nucleus is apparent, but in such cases I always failed to observe the dark striæ in the cell.

The existence of basal cells in the structureless border of the tunica propria, which M. Schultze has described, is questionable to me. I am unable to discover them even in very thin sections taken in situ. On one occasion only, in a large Salmon, I believed that a tendency to striation on the basal border might be considered

* Bulletin de l'Académie impérial des sciences de St. Pétersbourg.

as a row of cells. If the entire epithelial lining be separated from the tunica propria, no regular row of cells resting on the basal border is to be perceived, nor can regular rows of cells be recognized on the isolated layer of nerve-epithelium. M. Schultze has also already informed us that the basal cells did not occur in the entire extent of the comb of the crista acustica, but rather on the contiguous portions.

When now the fine nerve-fibres, which are by no means to be distinguished from the isolated axis-cylinders, enter the loose epithelial tunic, numerous anastomoses take place, and thus a nerve-network originates which has abundant tumefactions, both at the commissures and also in the fine fibrillæ. Once I succeeded in obtaining an admirable view of the plexus. Still, however, the nature of the variously formed swellings was questionable to me; for I am unable to regard these as ganglionic cells, as Reich has done, though quite recently observations are accumulating pointing to the fact that nucleated enlargements on the fine nerve-fibres are to be regarded as gangliform elementary elements, as in the granule layer of the retina.

The fibres pass onward from the fine network of nerves, dispose themselves vertically in the epithelium, and I believe that, supported by numerous observations, I may claim that the threads which enter the spindle-shaped cells represent the continuation of nerves. And if the dark striæ and the nucleus of the spindle cells are to be regarded as nervous formations because they color themselves dark in osmic acid, the auditory hairs can also be taken for gradually tapering prolongations of the flask-cells. These pass between the columnar cells supporting them, and, indeed, at those points where the angles of the polygonal cells meet. If the auditory hairs do not assume a black color, they certainly do show a brown hue sooner than any other tissue on the wall of the ampulla.

Thus we should have among the nerve epithelia of the ampullæ and saccules a number of cylindrical supporting cells, which develop spaces and fine canals between them for the reception of these spindle-shaped nerve-cells, which might be regarded as bearers of the terminal organs of vestibular nerves. I must mention here that F. E. Schultze has observed in Sea-gudgeons (Gobius niger?) that the primitive nerve fibres are directly continuous with the auditory hairs.

From the drawing furnished by this author it would appear that the epithelial cells had not yet become visible, owing to the early stage of development in the animals examined.

M. Schultze and C. Hasse affirm that, in the neighborhood of the nerve-hill of the crista acustica and macula acustica, cells stellate in form or containing pigment appear in various classes of animals. These bodies are placed between the simple columnar cells of the sloping sides of the nerve-hill. A more comprehensive statement in regard to their special arrangement is to be found in the excellent works of the two authors.

As for the auditory hairs, Ecker, Reich, and Leydig were the first to detect the existence of ciliated cells in the membranous labyrinth. M. Schultze, however, was the first to acquaint us with the true nature of these hairs. This investigation has furnished a proof that they are long, stiff, gradually tapering fibres, whose broader bases border the nerve-epithelium, and whose finely pointed extremities are surrounded by the endolymph, even if, as I suppose, they are not covered by a curiously organized cap.

As for the formation which Leydig has observed and sketched in the ampulla of the Pigeon, M. Schultze and I regard it as a collection of epithelial cells detached from the crista acustica and its vicinity. In Fishes and Birds, however, I have found an especial structure, delicate and composed of fine cells, which exists at a point corresponding with the ampullar ridge,

where the auditory hairs have their seat, but the precise relations of which I have thus far failed to get a satisfactory notion of.

The length of the auditory hairs in the Ray amount, according to M. Schultze, to 0.04‴ P. They are placed at regular intervals apart, and change their contour and appearance very rapidly under the action of various reagents.

Though the greatest care has been exercised in my manipulations, I have uniformly found in Mammals, Fishes, and Frogs that the basal portion of the auditory hairs was thicker than Schultze has described and drawn it.

Fig. 401.

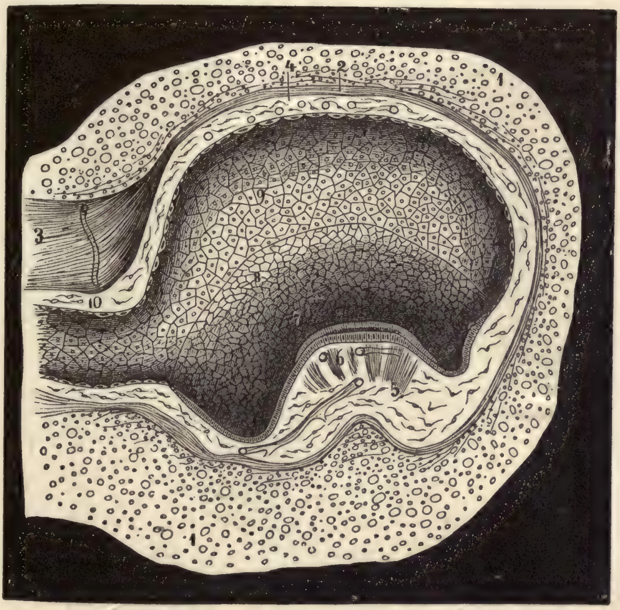

Fig. 401. **Longitudinal section through the ampulla of the Bird.** 1, bony wall; 2, periosteum; 3, free space between the bony and membranous canals; 4, wall of the ampulla adjoining the bone; 5, thickened crista acustica; 6, nerve fibres; 7, cylindrical floor cells about the nerve-hill; 8, line of demarcation between cylindrical and pavement cells; 9, flattened epithelium; 10, transition from ampulla to membranous canal.

The difference in the course of the nerves in the moderately thickened tunica propria of the maculæ acusticæ of the saccules amounts to this, as Henle has stated, that an actual linear course does not exist, as in the ampullar ridge. In other respects the same histological relation between nerve and epithelium is to be recognized here as in the ampulla.

Especially striking to the eye are the vesicular, structureless formations which appear in close rows both in the auditory hairs of the crista acustica and also in the planum semilunare. I have seen them best in osmic acid preparations of Cyprinus. In this animal they represent an uneven border on the inner surface of the epithelium, over its entire extent (fig. 402).

In these Fishes the auditory hairs seem, under certain conditions, to be cemented together by a glutinous material, for sometimes we observe in

them a regularly formed conical eminence (cupola terminalis) on the epithelial border of the ampullar ridge (fig. 402), and this, in some of my preparations, occupies more than two-thirds of the ampullar space. It has a slightly striated character, and the striæ run parallel from the base to the apex of the cone. Still these striæ do not appear to traverse all points of the hill, for by focalizing a certain point in its centre a finely granulated substance appears. On several occasions I believed that I had seen it covered by a hood formed of delicate cells. Lang has denied the existence of auditory hairs in the Cyprinoids, and, instead, has described the hill as the terminal apparatus of the ampullar ridge. Now I believe that in this hill the auditory hairs are cemented together, but sometimes very careful examination is required to detect this condition.

Fig. 402.

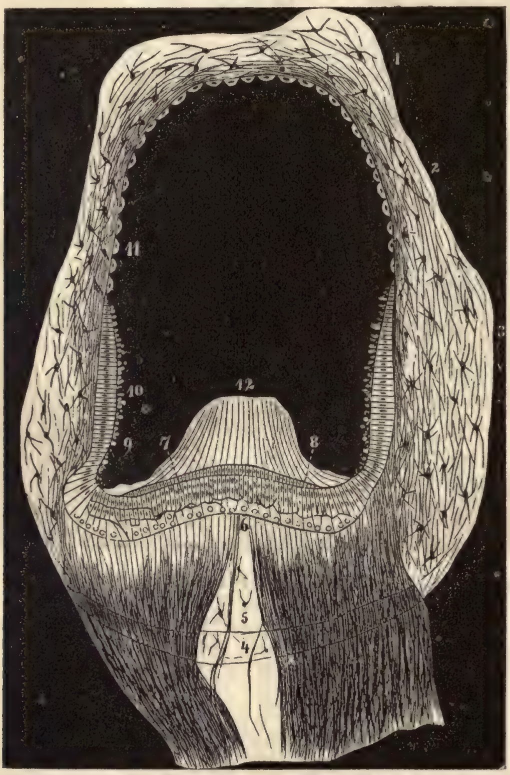

Fig. 402. Transverse section through the ampulla of Cyprinus carpio. 1, ampullar roof; 2, lateral wall of the ampulla; 3, thickened portion of the lateral wall corresponding to the planum semilunare; 4, 5, 6, floor of the ampulla crowded with nerves; 7, nerve epithelium; 8, columnar cells; 9, planum semi-lunare; 10, structureless formations lodged on the epithelium; 11, flattened epithelium; 12, cupola terminalis.

Finally, there still remain two apparatuses of the saccules which must be mentioned. They are :—

First. The Aqueductus vestibuli, and

Second. The Canalis reuniens.

Böttcher has recently drawn attention to the first.

The process in the bony Aqueductus vestibuli, which extends from the posterior surface of the pars petrosa towards the vestibulum, has also been known and described for ages as the Aqueductus vestibuli. Böttcher has recognized in this process an epithelial canal surrounded by a nucleated connective tissue, and invested, on its uneven inner surface, with a vascular (?) flattened epithelium, and very similar to the stria vascularis of the cochlea.

The simple canal lying in the aqueduct ends, on the posterior surface of the pars petrosa, with an abrupt enlargement, and in the vicinity of the saccules, divides into two hollow limbs, of which one is continuous with the sacculus rotundus, the other with the utricle. The cavities of the two saccules appear thus in mutual intercommunication. On cross-section of the Aqueductus vestibuli I have observed in a portion of its wall a pretty large plexus of vessels, so that Hyrtl's statement that it is designed for the support of the veins must claim our support.

The canalis reuniens is only limited to the round sacculus. It was discovered by Hensen, and confirmed by Von Reichert, Henle, and myself. It is attached to the periosteum, and only differs histologically from the saccule wall in having a finer character. This canaliculus establishes a communication between the round saccule and the ductus cochlearis, so that the former represents the blind vestibular end of the most important cochlear division of the labyrinth, just as the utricle forms the blind vestibular end of the membranous labyrinth.

5. *Otoliths.*

The otoliths enclosed in the albuminous endolymph of the membranous labyrinth exhibit striking differences as to consistency, size, and form, in different animals. They are held pretty firmly together by a clear, tough substance. In Reptiles and osseous Fishes these bodies are beautifully formed, and have a considerable size, while in Birds, Mammals, and Man, they appear either in the amorphous condition or as rhombic, hexagonal, or small octagonal crystals. In one and the same animal, however, otoliths of varying size and form are observed. Three or four otoliths of most beautiful form are found in the osseous Fishes, where they have a fixed position, both in the saccule and in the ampullæ. In Man and Mammals they are seen as white spots on the maculæ acusticæ, and, both here as well as in the other animals, are held firmly in place by a tough gelatinous substance, which Lang, in describing the Cyprinoids, has regarded as a fenestrated membrane proper. (According to Kölliker it is a cuticular formation.)

Both Deiters and Hasse assert that a fenestrated cuticular formation rests on the inner surface of the columnar epithelial cells in the stone sac of the Frog, by which contact with the otoliths was prevented. This I have seen very beautifully in cross-sections through the Frog's ear in situ. The otoliths are formed essentially of carbonate of lime; but, according to Henle, when treated with an acid, a residue remains which consists of organic substance (otolith cartilage). Leydig has observed, at the poles of the otoliths in the Mountain Cock (Auerhahn), when treated with bichromate of potash, curious markings, which, becoming acuminate, are directed inwards (fig. 403, 10).

Mention must be made of the fact, that in Man and Birds, both in the membranous and semicircular canals, and especially in the horizontal, and also (as Hyrtl adds) in the serum of the cochlear passages, otoliths are

observed in great numbers, even at the time when the vestibule remained intact. In this case it cannot certainly be claimed that they have reached the passages from the utricle.

6. *The Oval Window and its Connection with the Base of the Stirrup.*

Most authors describe the insertion of the base of the stirrup into the oval window as if it were an exceedingly simple matter, though I find it a pretty complicated mechanism, and a fact which Soemmering,* too, has

Fig. 403.

Fig. 403. Otoliths from different classes of animals. 1, from the Goat; 2, from the Herring; 3, from the Sea-Devil; 4, from the Mackerel; 5, from Pterois volitans (after Breschet); 6, from the Pike; 7, from Cyprinus carpio; 8, from the Ray (after Leydig); 9, from Scymnus lichia (after Leydig); 10, from the Mountain Cock (Auerhahn, after Leydig).

alluded to, for he says "that the base of the stirrup is attached to the semi-oval window by a delicate articular capsule." Now, whether Soemmering, under the name of articular capsule, meant to imply that there was an actual articular connection, or only a fibrous lamella, similar to a fibrous articular capsule, is impossible to make out, from the short notice he makes of the matter. Several authors speak of a simple fibrous connection which they characterize as the ligamentum orbiculare baseos stapedis.

It was reserved for the indefatigable Toynbee to furnish a more exact description of the union between the footplate of the stirrup and the oval window.

Toynbee † first drew attention to the difference in form, which is certainly important from a physiological point of view, between the anterior and posterior border of the base of the stirrup. This author also was the first to describe the hyaline cartilage at the oval window and base of the stirrup.

* Vom Bau des menschlichen Körper's. Frankfurt, 1796. Part 11, page 12.
† *British and Foreign Medico-Chirurgical Review*, 1853.

A comparison of the anterior with the posterior end of the base of the stirrup, in successful preparations, shows that, besides the increase in thickness observed in these places, posteriorly the pretty high surface of contact forms almost a right angle with the vestibular surface of the foot-plate, and that the foot-plate juts off from the posterior arm of the stirrup in the form of a process. (Fig. 404.)

The surface of contact on the anterior margin of the foot-plate appears to form an acute angle with the vestibular surface, is somewhat lower than the posterior, and the entire anterior extremity, which overrides the corresponding arm, appears somewhat longer than the posterior, and it may certainly be claimed that, on account of the oblique surface, and the greater length of the anterior border of the foot-plate, a certain resistance is opposed to the action of the voluntary stapedius muscle.

The borders of the base of the stirrup, already mentioned, are covered

Fig. 404.

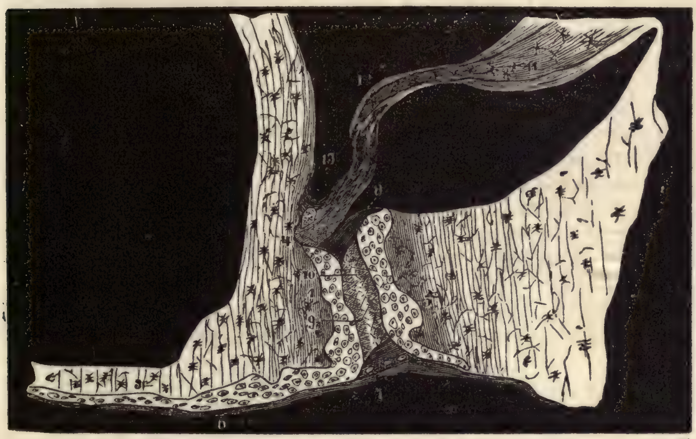

Fig. 404. Horizontal cross-section through the base of the stirrup which is connected with the posterior margin of the oval window. 1, bony margin of the base, with covering of hyaline cartilage; 3, thin, bony lamella of the base; 4, angle between the arm of the stirrup and the prominent border of the base; 5, posterior margin of the oval window, with the hyaline cartilaginous covering; 6, cartilage on the vestibular surface of the base, with the perichondrium; 7, ligamentum baseos stapedis vestibulare; 8, ligamentum baseos stapedis tympanicum; 9, elastic fibre layer; 10, interspaces between the fibres; 11, bony ridge; 12 and 13, musculus fixator baseos stapedis.

with a hyaline lamella of cartilage, which exhibits on cross-section a diameter varying between 0.012 and 0.024 millim. Where the surface of the bone is uneven, the hyaline cartilaginous substance sinks in, to produce here, as in the other bony connections, a uniform evenness of surface. Still, not only is the anterior and posterior border of the stapedial foot-plate covered with this cartilage, but the entire vestibular surface of the stirrup is also overspread in the same way.

At the last-mentioned point the cartilage is covered with a nucleated fibrous tissue, the perichondrium, which ranks among the investing tissues of the vestibule.

The homogeneous basis substance of the cartilage is distinguished from

the contiguous bone tissue by its yellowish color; in stained preparations the rounded cartilage cells contrast very markedly with the nearly colorless inter-cellular substance, owing to the deep color their nuclei assume.

In the middle of the vestibular surface of the base of the stirrup the form of the cartilage cells changes, for here they assume a lengthened form, and are all parallel with the longest diameter. The edge of the oval window, too, is provided with a hyaline covering of cartilage. On the posterior border, it is as stout as the corresponding layer on the confronting surface of the stirrup; anteriorly, however, it measures from 0.040 to 0.048 millim. Towards the cavity of the tympanum this cartilage has a more distinct outline than in the vestibule, where it passes out over the border of the oval window, and, tapering down, levels the surface of the vestibule for a short distance.

On the hyaline cartilage, both at the oval window and also along the margin of the stapedial foot-plate, there is a uniformly stout, essentially elastic fibrous layer, which is very thick and attracts the eye by the deep coloring it shows in stained preparations. These fibres run out from the cartilage to meet one another, and at the point where both are in contact a reticulated system is formed by a net-like union of the bundles. The interspaces are filled with fluid.

In the direction of the vestibule and tympanic cavity the thick elastic tissue extends from one cartilage to another, and forms a ligamentum orbiculare baseos stapedis vestibulare, and within the tympanic cavity a weaker ligamentum orbiculare baseos stapedis tympanicum.

The latter is connected with the mucous membrane of the tympanum, without, however, being so sharply separated from the surrounding parts as is represented in fig. 405.

Along the upper and lower margin of the base of the stirrup the attachment changes its character so far that the uniformly thick border of the base, which is pretty prominent near the tympanic cavity, has somewhat smaller surfaces of contact than those described in the anterior and posterior end. Here also, however, there are cartilaginous investments, which become somewhat stouter as they approach the middle of the vestibular surface of the base. Union with the cartilaginous covering takes place through an elastic fibre layer, in whose centre the interspaces which communicate with one another appear more sparsely than in the anterior and posterior border.

The connection of the stirrup with the oval window is neither a pure syndesmosis nor a synchondrosis, but a form of union exists, which, to classify it accurately under the different varieties of joints, is most nearly allied to the so-called semi-articulations.

It only differs from these articulations in the fact that a larger number of inter-communicating cavities exist, while the semi-articulations are characterized by an irregularly defined formation of cavities.

Now apart from the special designation of this attachment we wish the fact emphasized, that the stapedial foot-plate is curiously inserted in the oval window, a fact which Helmholtz has established experimentally. Helmholtz proved that the capacity of motion in the stapedial base is very small, the entire amount of excursion in the stapes being from $\frac{1}{18}$ to $\frac{1}{24}$ millim. According to previous statements as to the connection between the stirrup with the oval window, a greater capacity for motion had to be claimed.

Yet the diameters of the bony oval window are so far diminished in all directions by the elastic cushion, the hyaline cartilage, that the basis, with

its cartilage and its broad surfaces of contact, fits in so closely that little space is left for play.

I have still to allude to another arrangement on the tympanic surface of the base of the stirrup, and which, in view of the researches thus far come under my notice, I should like to regard as a vegetative muscle, the *musculus fixator baseos stapedis.* In the tympanic cavity, one millimetre distant from the oval window along the posterior and upper border, there is a thin ridge of bone which has, in transverse section, a diameter of 0.080 millim. This on surface view appears as a slight curved ridge, shaped like the letter S, and ends with an obtuse angle, which confronts the prominent border of the base of the stirrup. Its significance is only apparent on cross-sections. The relation which the mucous membrane bears to this bony ridge is the same as it has to all other prominent formations in the tympanic cavity.

Fig. 405.

Fig. 405. Horizontal section through the anterior border of the base of the stirrup, at its junction with the oval window.

1, Jagged border of the base with its cartilage ; 2, footplate ; 3, anterior arm ; 4, border of its oval window with the hyaline cartilage ; 5, ligamentum baseos stapedis tympanicum ; 6, ligamentum baseos stapedis vestibulare ; 7, layer of elastic fibres at the oval window ; 8, the same at the base of the stirrup ; 9, reticulated system in the centre of the fibrous layer. Both margins at the base are not so jagged as in the accompanying diagram.

The direct continuation of this bony ridge appears to be a *yellow-colored firm tissue*, which is attached in the angle between the side of the stirrup and the somewhat expanded portion of the foot-plate. This tissue, however, is not only connected with the bone, but with the cartilaginous covering too (fig. 404). Now, on cross-sections that have been stained we observe long colored striæ, which, when isolated, prove to be spindle-shaped cells ; at the present time I can only regard them as fibre cells.

The attachment of the fixator baseos stapedis is not only confined to the posterior end of the base of the stirrup, though here it is strongest, but extends also towards the upper border. and in virtue of the direction of its action may be regarded as the antagonist of the voluntary stapedius muscle ; for it fixes the base at that point where it is forced against the vestibule through the one-sided working of the musculus stapedius.

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IV. AUDITORY NERVE AND COCHLEA.

By W. WALDEYER.

BRIEF SUMMARY OF THE COMPARATIVE ANATOMY AND EMBRYOLOGY.

The *apparatus of the semicircular canals* (utriculus and membranous semicircular canals), which has been treated of in the preceding chapter, is found in a perfect state of development in most of the Fishes; the second division, however, of the membranous labyrinth, the *apparatus of the cochlea*, belongs, in its full state of development only, to the higher classes of Vertebrates. The apparatus of the cochlea includes the *sacculus*, which in its histological character resembles more closely the utriculus (see preceding chapter), and a passage-way with blind termination which starts from the sacculus—the *ductus cochlearis*.

The first trace of a ductus cochlearis is found in the Osseous Fishes, in which, according to Hasse's (25) conclusive statement, a small diverticle of the sacculus (fig. 406, *I C*)—Breschet's (5) so-called *cysticula*—is to be regarded as a rudimentary cochlea.

In the Amphibia several divisions of the sacculus can be distinguished as belonging to the cochlea; these, however, with the exception of one small sac-like projection, which is rather more prominent than the rest, and corresponds to the cysticula of Fishes and the lagena of Birds, scarcely rise above the level of the wall of the sacculus (stone-sac); they are rather to be considered as single thickened portions of the wall of the sac [(Deiters (15), Hasse (24)], which are provided with special nerve-terminations.

A higher stage of development is found in the cochleal apparatus of Reptiles and Birds. In the former all the subdivisions of the cochlea rise above the level of the sacculus in the form of a conical appendage: this is particularly the case in Crocodiles, which in this respect most resemble Birds. In the latter the sacculus and utriculus, as Hasse has made probable (*Zeitschr. f. wiss. Zool.*, Bd. 17, p. 631), are fused into an alveus communis (fig. 406, *II*, *US*); the canal of the cochlea (*C*) is very much lengthened, and has several subdivisions: the commencing portion or the cochlea proper (*UC*) and the flask-shaped terminal portion—the lagena (*L*) (Windischmann). Here, too, we meet with the first indication of a spiral course in the cochleal canal. The latter communicates with the alveus by means of a narrow passage, the *canalis reuniens* (Hensen), which, according to Hasse's experience, seems often in full-grown Birds to become obliterated—at all events, there is sometimes found only a small vessel in its stead.

Fig. 406, *III* gives a diagrammatic representation of the Mammalian labyrinth; the apparatus of the semicircular canals and the cochleal portion communicate with each other only by way of the *aquæductus vestibuli* (*R*) (see preceding chapter) (Boettcher (3)). The ductus cochlearis (*C*), it will be seen, has attained extraordinary proportions, and constitutes the chief bulk of the labyrinth; it has also, as in the case of Birds, almost entirely emancipated itself from the sacculus, with which it is connected only by means of the narrow canalis reuniens (*Cr*). The canalis reuniens starts from the vestibular wall of the ductus, the membrana Reissneri (see farther on); it empties into the cochleal canal at nearly a right angle, and just beyond it lies the *vestibular blind sac* (Reichert) (*V*). The other end of the

cochleal canal also ends abruptly—*blind sac of the cupola* (Reichert) (K). The canalis reuniens and both blind sacs are lined with only a short cylindrical epithelium, and receive no fibres from the N. acusticus. The cochleal canal,

Fig. 406.

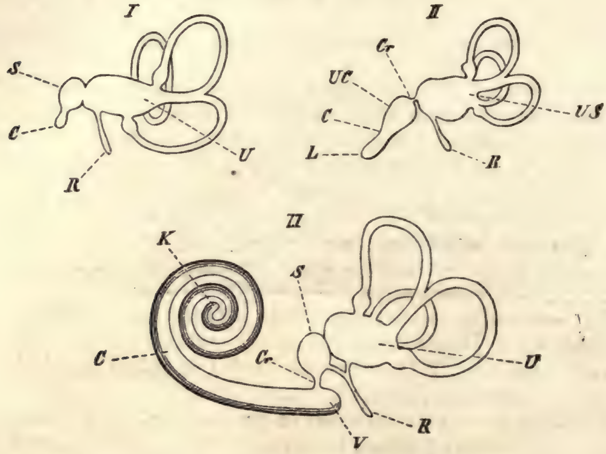

Fig. 406. Three diagrammatic drawings to illustrate the relations of the labyrinth of the ear in the Vertebrated series. *I*, diagram of the Fish's labyrinth; *U*, utriculus with semicircular canals; *S*, sacculus; *C*, cysticula; *R*, aquæductus vestibuli; *II*, diagram of the Bird's labyrinth; *US*, alveus communis; *C*, cochlea; *UC*, commencing portion of the cochlea; *L*, lagena; *Cr*, canalis reuniens; *R*, same as above; *III*, diagram of the Mammalian labyrinth; *U*, *S*, *Cr*, same as above; *R*, aquæductus vestibuli, dividing into two arms for the utriculus and sacculus; *C*, ductus cochlearis, with *V*, the vestibular blind sac, and *K*, the blind sac of the cupola.

which really merits its name only in Mammals, winds spirally round an osseous axis, the *modiolus*. The number of turns varies in the different species from 1½ to 5; in some varieties, as in the Planorbis (Cetacea), the turns lie more in one plane, while in others, as the Clausilia (Guinea-pig) for instance, they wind round the modiolus at a steep angle—flat- and steep-coiled cochleæ.

For details concerning the sacculus I shall refer the reader to the preceding chapter. In consideration, however, of the fact that the structure of the cochlea is somewhat complicated, I deem it advisable to preface the histological description with a short account of the osseous house of the cochlea, and of the situation of the ductus cochlearis, together with a sketch of the development of these parts. I shall commence with the cochlea of Mammals and of Man.

The median section through the axis of the Human cochleal house—fig. 407—reveals, embedded in the hard substance of the petrous bone, a tubular canal, which, with constantly diminishing calibre, coils round the osseous axis, and above ends blindly in the so-called cupola; the axis itself, as it approaches the cupola, constantly diminishes in size. This canal is traversed throughout its entire length by a septum, partly osseous, partly membranous—the *lamina spiralis*—which on the outer side splits up into two layers, that are attached to the bony wall of the cochlea, and enclose the ductus cochlearis (fig. 407, *L sp*). In this way the bony cochleal canal

is divided by the ductus cochlearis and its two attachments—the osseous to the modiolus, and the membranous to the outer wall—into two chambers, the *scala tympani* (ST) and the *scala vestibuli* (SV), which communicate with each other only in the cupola, through a fine opening—Breschet's *helicotrema.* The scala tympani terminates blindly, being separated from the tympanic cavity by the membrane of the fenestra rotunda; the scala vesti-

Fig. 407.

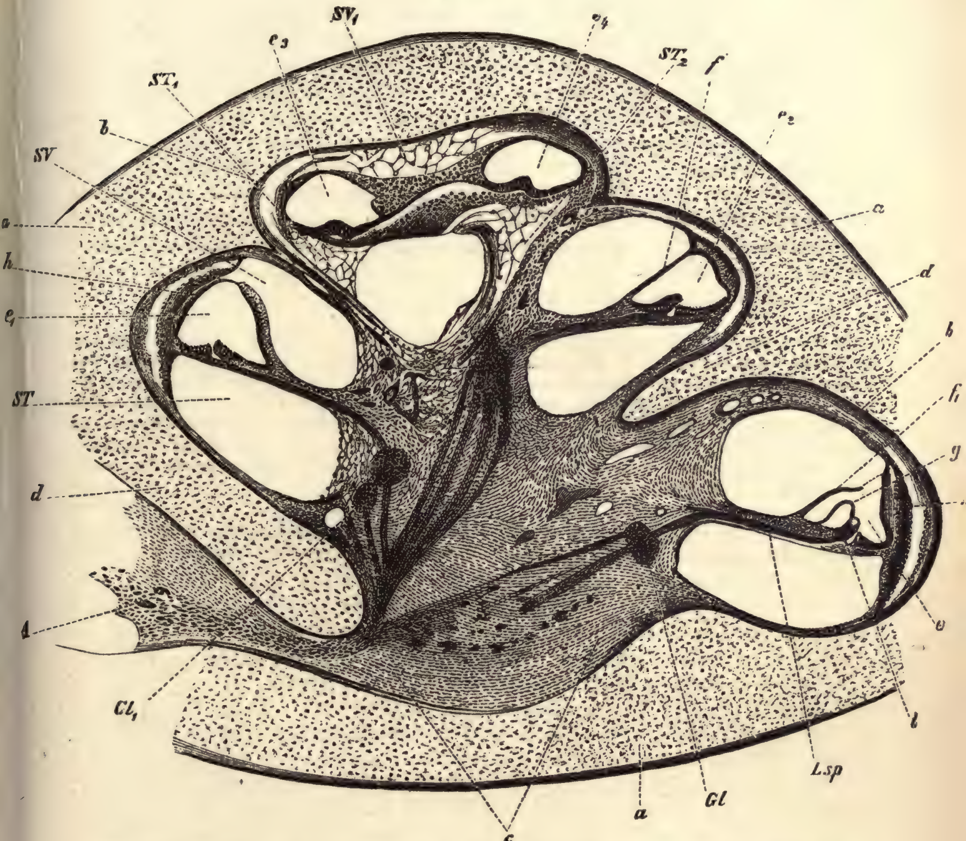

Fig. 407. Section of the cochlea of a Human embryo at the fourth month. $\frac{30}{1}$. a, a, a, cartilaginous incasement of the cochlea; b, b, perichondrium; c, mucoid tissue matrix of the modiolus; d, d, cartilaginous septa of the individual turns of the cochlea; e—e_4, sections of the ductus cochlearis; f, f_1, Reissner's membrane; g, membrana tectoria, somewhat lifted up from the subjacent parts; h, rudiment of the stria vascularis; i, rudiment of the subsequent organ of Corti; $L\,sp$, lamina spiralis; Gl, Gl_1, ganglion spirale with various efferent and afferent bundles of nerves; ST, scala tympani: SV, scala vestibuli; ST_1, SV_1, ST_2, mucoid tissue where later the scalæ of the last cochleal turn will be.

buli communicates directly with the perilymphatic space of the vestibular sacs.—The situation of the duct in the cochleal house corresponds therefore to that of the membranous semicircular canals and sacs in the remaining portion of the labyrinth (see preceding chapter). Like these, it is at-

tached eccentrically to the outer wall of the canal, and indeed on two sides.

The medial (with reference to the axis) plate of attachment, which at the same time carries the nerves, is here drawn out to a great length, and is ossified (*lamina spiralis ossea*); the lateral plate of attachment, which chiefly carries vessels (fig. 407, the connective tissue between *h* and *b*; figs. 408 and 409, *e e*), forms, as seen in cross-section, a thick semi-lunar cushion —Kölliker's *ligamentum spirale* (see page 1020).

The ductus cochlearis (fig. 407, e–e_4, figs. 408 and 409, *D. C.*) represents in the Adult (on cross-section) a three-sided canal-shaped space, which is shut in on all sides by a connective-tissue membrana propria: on the tympanic side, by the *membrana basilaris* (*f–L. Sp.*), which is united to the *crista spiralis* (*R–Cr.*, figs. 408 and 409) in the *sulcus spiralis internus* (*S, Sp, i*)—the entire tympanic side is understood to extend from the letter *R* to the letters *L. Sp.*; on the vestibular side, by Reissner's membrane ($f\,f_1$, fig. 407, R–R_1, fig. 408); laterally, by a layer of vascular connective tissue which, through the above-mentioned semi-lunar cushion of connective tissue, is continuous with the periosteum of the cochlea (*e e*, figs. 408 and 409). On the inner side the membrana Reissneri and the crista spiralis unite at a more or less acute angle.

In the remainder of this article we shall term all the surfaces that look toward the modiolus of the cochlea "inner" (medial), and those that are turned toward the outer wall of the bony cochleal canal "outer" (lateral). Whatever runs in the direction from the axis to the outer wall we shall call "radial;" and, on the other hand, we shall employ the term "spiral" for whatever pursues the same course as the coils of the cochlea (Henle). Finally, we shall employ the terms "vestibular" and "tympanal" respectively for those surfaces which look toward the scala vestibuli and scala tympani.*

In regard to the formation of the cochlea, I shall dismiss the subject with a very few words. In Human embryos of the 8th to the 10th week, three different histological elements may be distinctly made out in the region of the subsequent pars petrosa of the temporal bone: on the outermost side, a cartilaginous mass, which at this period is continuous with the rest of the cartilaginous basis of the skull; then, surrounded on all sides by the cartilage, a considerable deposit of embryonic mucoid tissue, in the midst of which the epithelial labyrinthine vesicle is embedded. From that portion of the vesicle, which corresponds later to the sacculus, there is developed in the Human embryo, before the eighth week even, a hollow epithelial bud which gradually penetrates farther and farther into the mucoid tissue: hindered, however, in its further growth by the surrounding firmer capsule, it turns itself round in its soft bed and pursues a spiral course. In one spot the cartilaginous capsule is not closed, and here the ramus cochlearis of the auditory nerve effects an entrance. In Human embryos at the third month the hollow epithelial bud—the rudimentary ductus cochlearis—is found to have already completed its turns; in embryos at the fourth month

* There can scarcely be found anywhere within an area so small such a rich and at the same time complicated nomenclature as in the anatomy of the cochlea. The confusion is not diminished by the custom—so prevalent among authors, but scarcely to be recommended—by which each one, who introduces to us a long-known structure with a new description, thinks he must at the same time give it a new name. Possibly the names used in this article will seem to those interested in this department as not unsuited to restore harmony. At all events there is scarcely a new word; and many superfluous terms, and others that are used for two different objects, have been omitted altogether.

the formation of the scalæ and parts contained within the ductus proper commences (fig. 407).

The scalæ are formed by the melting of the mucoid tissue on both sides of the ductus cochlearis (see fig. 407, where the mucoid tissue is still preserved in the last turn); that portion, however, which is to form the wall of separation between every two turns (a portion of the cartilaginous capsule, *d*, fig. 407, contributes also to its formation) becomes ossified. There remains furthermore a cord, which extends from the ductus to the mucoid-tissue axis, and in which even at an early date the fibres and ganglion cells of the N. acusticus make their appearance (*L. Sp.* and *Gl.* in fig. 407). This cord becomes ossified in part, that is, in the neighborhood of the axis (lamina spiralis ossea), and continues always to be united in a peculiar manner to the connective tissue membrana propria of the ductus—for the membrana propria can be demonstrated even at this period as a special layer. The membrana propria is developed from the mucoid tissue surrounding the epithelial tube in exactly the same manner as in the case of the theca of the Graafian follicle or the connective-tissue wall of the utriculus and semicircular canals. We always find the same process taking place wherever epithelial masses in the course of development find their way into a connective-tissue groundwork (see His—Entwickelung des Hühnchens, Leipzig, 1868). These epithelial structures appear to exert a formative irritation upon their connective-tissue surroundings, as a result of which there takes place immediately around the epithelial tube a prolific cell-growth, from which later the membranæ propriæ of the originally naked epithelial masses are formed. This is demonstrated, for the ductus cochlearis in particular, by the drawings of E. Rosenberg (49), the truthfulness of whose fig. 1, plate II. I can entirely corroborate. Finally, ossification also takes place in the mucoid-tissue axis of the cochlea, in which the fibres of the nerve lie embedded. In all the ossified portions we find traces of the former mucoid tissue in the shape of a delicate periosteum; even at an early period it is possible to distinguish along the inner wall of the cochleal house a special perichondrium, with which, however, at a later date the remains of the mucoid tissue of the scalæ become fused.

The epithelium of the ductus cochlearis (fig. 407, e–e_4) is genetically the same as that of the labyrinthine vesicle; hence, if we adopt Remak's views, we must refer its origin to the embryonic horny layer, a portion of which, it is said, projects diverticle-like into the rudimentary petrous bone. The remains of this diverticle-like protrusion may still be seen, as Böttcher (3) has recently demonstrated, in the epithelial lining of the aquæductus vestibuli (recessus labyrinthi Reissner), which continues to exist even in Adults, and which, in the Plagiostomata, empties at the external surface of the skin by a fine opening. Stricker (64), Schenk (63), and Torök (65) have shown that in the Batrachia it is not so much the horny layer, but rather Stricker's so-called "sensorial layer," lying immediately beneath the latter, that gives origin, by a diverticle-like protrusion, to the auditory labyrinth—a view which has recently been confirmed by Van Bambeke (58). This would render the unity of development complete in the case of the labyrinth, the retina, and the vesicle of smell, all of which, together with the central nervous system, must be referred for their origin to the sensorial layer. From the involuted epithelial lining of the ductus cochlearis is developed, as Kölliker has shown, the most essential part of the cochlea—the organ of Corti. Farther on in the course of the description I shall return to the most important details of this process, so far at least as they are known to us at present.

From this outline sketch of the comparative anatomy and embryology of the subject, we obtain the necessary basis for a correct conception of the histology of the cochlea. We learn in the first place that the original soft parts of the cochlea are distinct from their osseous capsule, which belongs to the petrous bone; we learn, too, that the scalæ, are secondary formations around the principal canal of the cochlea, the ductus cochlearis, whose epithelial lining proves eventually to be the germ-centre, so to speak, of the entire apparatus. The most natural order, therefore, in which to group the different sections of our histological description would be the following:—The osseous cochleal incasement with its periosteum; then the structures of the modiolus and lamina spiralis; the scalæ, together with the parietal connective-tissue layer of the ductus cochlearis; and, finally, the epithelial lining of the latter. Then will follow very properly the description of the terminal expansion of the N. acusticus, in which the necessary details concerning the histology of the trunk of the auditory nerve should also be included.

Bony Capsule of the Cochlea; Membrana Propria of the Ductus Cochlearis.

In reference to the *bony capsule* of the cochlea, it will be sufficient to mention the compact structure of its inner layers, which are poor in bone cells, and constitute a sort of tabula vitrea. On the other hand those portions of the cochlea which represent ossified mucoid tissue—the modiolus and lamina spiralis—possess a more porous character; they carry within their substance numerous small medullary spaces, by the side of the canals for the vessels and nerves. One of these vessels—the *canalis ganglionaris* (Claudius, Vietor [55]), discovered by Rosenthal—gives lodgment to the *ganglion spirale* of the N. acusticus, and is situated usually in the commencing portion of the lamina spiralis, encircling with it the modiolus (figs. 407 and 409).

In Man this canal is traversed by numerous bone-trabeculæ, so that, strictly speaking, it represents a canal-shaped cavernous space, in whose meshes the ganglion cells and nerve fibres lie.

We have already referred to the relation of the periosteum of the wall of the cochlea to the ductus cochlearis. In regard to all other points, the description of the labyrinthine periosteum given in the preceding chapter may be consulted; I would like, however, to call special attention again to the frequent occurrence here of stellate pigment cells, similar to the stroma cells of the choroidea; in Man and in the Rat these cells are found in the greatest numbers. The inner surface of the periosteum is covered everywhere—with the exception of the tympanal surface of the membrana basilaris, where I was equally as unsuccessful as Kölliker (30) in proving their existence—with a single layer of large, flattened, nucleated cells, which, when treated by the silver method, yield the same outlines as those obtained in lymph sacs or serous membranes. Luschka (Structur der serösen Häute, Tübingen, 1851) has already mentioned these appearances on serous membranes; see also the statements of Reichert (44–45). By the investigations of Schwalbe,* moreover, it has been determined that the scalæ may properly be considered as a lymphatic cavity, corresponding more especially to the perichoroideal space of the bulbus oculi or to the arachnoid space of the brain. See also Kölliker's account (62, 34).

The membrane of the *fenestra rotunda* belongs both to the mucous membrane of the tympanic cavity and to the periosteum of the cochlea; it is found accordingly to consist of two layers, which are composed of delicately

* *Centralblatt für die medicin. Wissensch.* 1869.

fibrillated connective tissue. The tympanic layer is the thicker of the two, is traversed by numerous vessels, and covered by the epithelium of the tympanic cavity; the vestibular layer, which faces the scala vestibuli, passes continuously into the periosteum of the first cochleal turn.

Fig. 408.

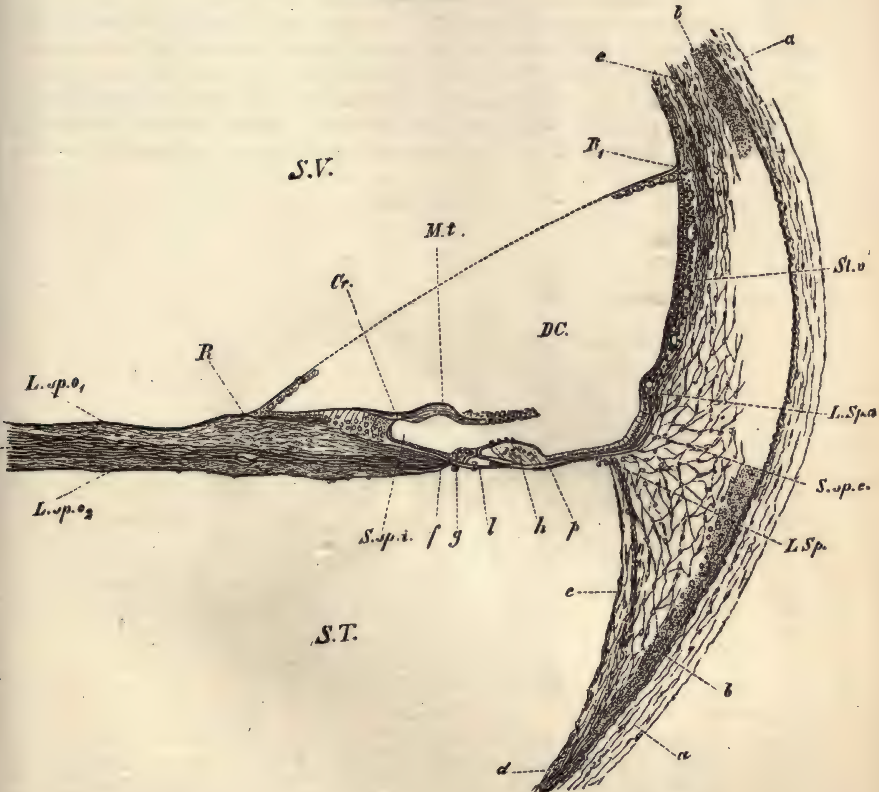

Fig. 408. Vertical section through the first turn of the cochlea, from a 1½ yr. old Child. $\frac{100}{1}$. (The membrana tectoria was drawn from another specimen of the same cochlea, and inserted here in its proper place.) *S. V.* Scala vestibuli. *S. T.* Scala tympani. *D. C.* Ductus cochlearis. *L. sp.* o_1, Vestibular, *L. sp.* o_2, Tympanal lamellæ of the lamina spiralis ossea. *N.* Auditory nerve. *a*, *a*, Osseous wall of the cochlea. *b*, *b*, Periosteum. *e*, *e*, Connective-tissue cushion (Kölliker's ligamentum spirale), in one place separated from the osseous wall, while in the neighborhood of the ductus cochlearis it is condensed to form a special fibrous boundary wall of the duct. *St. v.*, Stria vascularis. *d*, Locality in which the periosteum and the connective tissue of the cushion become merged into one. *L. Sp.*, Ligamentum spirale of Henle. *L. Sp. a.* Ligamentum spirale accessorium with the vas prominens. *S. sp. e.*, Sulcus spiralis externus. *R*–R_1, Reissner's membrane, both ends of which only are preserved. *R – Cr.*, Crista spiralis, whose most projecting portion, *Cr.* (auditory teeth), is seen in transverse section. *M. t.*, Membrana tectoria. *S. sp. i.*, Sulcus spiralis internus. *f.* Point of emergence of the nerves (habenula perforata). *f–L. Sp.*, Membrana basilaris. *f–p*, Organ of Corti. *Cr–p*, Zona denticulata. *g–h*, Zona arcuata. *p–L. Sp.*, Zona pectinata with epithelium. *g.* Region of the inner hair cells (inner slope). *l*, Thinnest portion of the membrana basilaris, beneath the arch of Corti. *h*, Region of the outer hair cells (outer slope).

It will also be proper in this place to make brief mention of the *aquæductus cochleæ*, which, according to the views hitherto prevalent (see particularly Hensen (27), and Henle (26)), carries, besides a process of connective tissue from the dura mater, but a single vessel, which empties into the V. jugularis. The orifice of the aquæductus is in the immediate neighborhood of the commencing portion of the scala tympani.

Before entering upon the description of the most important part of the cochlea, the *ductus cochlearis*, let us take a hasty glance at the component elements as drawn in the transverse sections—figs. 408 and 409.

In connection with what I have already said on page 1016, concerning the position, form, and surroundings of the ductus, I would remark in the first place that the vestibular wall, the *membrana Reissneri*, is inserted on the

Fig. 409.

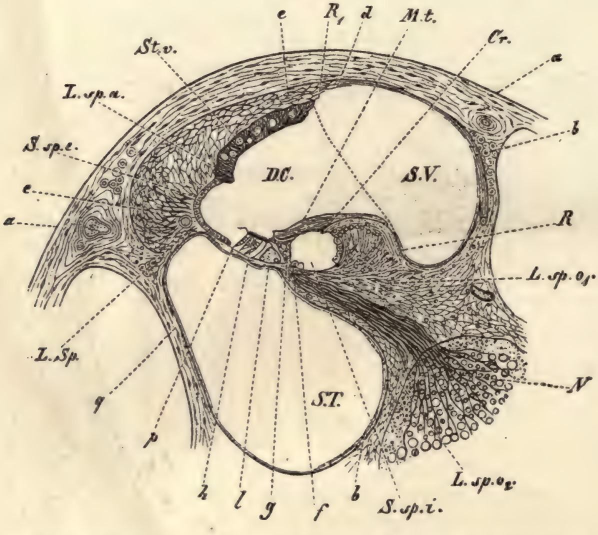

Fig. 409. Vertical section through the second turn of the cochlea of Vesperugo noctula. (Membrana tectoria drawn from another preparation and inserted here.) $\frac{100}{1}$. *N.* Cochleal nerve, with a portion of the ganglion spirale. *e, e.* Connective-tissue cushion, more firmly united with the periosteum than in fig. 408. *L. Sp.* Lig. spirale, of homogeneous consistency; immediately to the outside of it, a blood-vessel. *R–R*$_1$, Reissner's membrane, designated only by a dotted line. *h*, Outer slope, with the three outer hair cells in situ. The inner hair cells, as well as the epithelium of the sulcus spiralis internus, have not been perfectly preserved. The remaining letters are used in the same manner as in fig. 408.

outer side into the semi-lunar connective-tissue cushion (*e, e*); the point of insertion—*angulus vestibularis* (*R*$_1$)—is marked by the presence of a small prominence (Henle). The outer point of insertion of the tympanic wall (*R–L. Sp.*) is also characterized by a well-marked prominence—*ligamentum spirale* (*L. Sp.*)—which in transverse section is triangular in shape. Between these two prominences lies the outer wall of the ductus, in which we can distinguish, in the first place, the vascular *stria vascularis* (*St. v.*); then a third small elevation—the *lig. spirale accessorium* (*L. sp. a.*)—with a vessel in its midst, Hensen's *vas prominens*, the whole constituting the

tympanic boundary of the stria; and finally, between this elevation and the membrana basilaris, the *sulcus spiralis externus* (*S. sp. e.*). Perhaps the best place to draw a line of separation between the two principal portions of the tympanic wall, the *crista spiralis* and *membrana basilaris*, is the spot where the cochleal nerve emerges into the space of the ductus cochlearis. The crista spiralis (*R–f*) rests upon the outermost portion of the lamina spiralis ossea, and consists of two lips: the *labium vestibulare* (*c*, fig. 412) (Henle), whose sharp, prominent edge (*Cr*) projects into the ductus cochlearis; and the *labium tympanicum* (*a*, fig. 412) (Henle), which lies in the same plane with the membrana basilaris. These two lips include between them the *sulcus spiralis internus* (*S. sp. i.*). The *organ of Corti* lies stretched upon the membrana basilaris, from the point where the nerves emerge (*a*, fig. 410), to about the middle of its length; beyond this point, as everywhere else over the inner wall, there is found a simple, short-cylindrical or cubical epithelium.

Fig. 410.

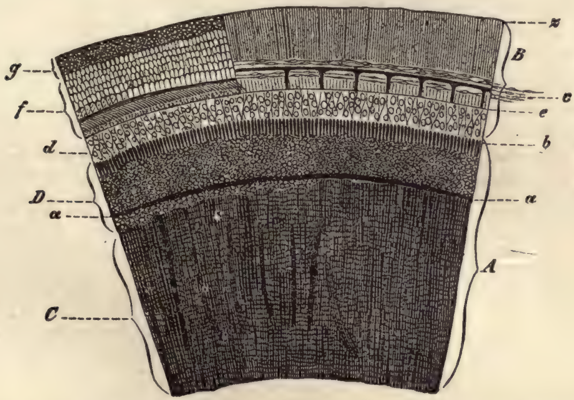

Fig. 410. A surface view (from the vestibular side) of the lamina spiralis of the Human being: second turn. $\frac{30}{1}$. Taken from a Woman 28 years old. Reissner's membrane and the membrana tectoria removed. *A*, Lamina spiralis ossea. *B*, Lamina spiralis membranacea. *C*, Dark zone of the lamina spiralis ossea (covered only by a thin periosteum, and the endothelium of the scala vestibuli). *D*, Crista spiralis, brighter in appearance than the preceding; its projecting edge (*b*) carries the row of auditory teeth. *a*, line of insertion of Reissner's membrane; *a–z*, that portion of the lamina spiralis which belongs to the ductus cochlearis (tympanic wall of the ductus); *c*, vas spirale, shining through from the tympanic surface, and accompanied by delicate spiral bands of connective tissue; *d*, ground surface of the sulcus spiralis internus, with fibres that pursue a radial direction, shining through from the tympanic surface; *e*, line in which the openings lie from which the nerves emerge; *f*, organ of Corti; *g*, outer epithelium (*f* and *g* have been removed from the right half of the preparation).

If we look down upon the tympanic wall from the vestibular side, after the removal of Reissner's membrane, its several subdivisions will appear like so many spiral girdles or zones, of which fig. 410 gives a representation. The following terms, which were introduced by Todd-Bowman, Corti, Kölliker, and others of their time, refer to the parts here described: zona denticulata and pectinata, together with habenula denticulata, sulcata, perforata and arcuata, subdivisions of the zona denticulata, concerning which th

explanations of figs. 408, 409, 410, and 411 should be consulted. These terms, however, may now be considered as superseded by others.

According to my measurements (see appended table) the breadth of each of the three walls of the ductus cochlearis diminishes steadily though slowly in the direction of the cupola of the cochlea.

The *membrane of Reissner* consists of a thin, vascular connective-tissue basis-lamella, which, on the vestibular side, carries a serous endothelium composed of large cells, while on the tympanic side it is covered with an epithelium consisting of a single layer of cubical cells, arranged side by side (figs. 408 and 411).

The *outer wall* of the membranous cochleal canal (figs. 408 and 409 *e*, *e*) shows a more complicated condition of things. In the semilunar connective-tissue cushion, of which mention has frequently been made, we can easily distinguish three layers, especially in young individuals: to the inner side, the *membrana propria* of the ductus cochlearis, with the stria vascularis; to the outer side the periosteum; and between these two a loose connective tissue, which in embryos easily tears, and thus permits the ductus cochlearis to recede from the cochleal incasement. The stria vascularis is a part of the membrana propria, which is especially vascular. Scarcely any adventitial connective tissue can be found between the numerous capillaries; the epithelium, consisting of small cubical cells, lies almost directly upon the walls of the vessels. In a few places small loop-like vascular offshoots may be observed. These last are of uncommon size and frequency in Birds, where they are found in the cover of the ductus cochlearis, in the so-called *tegmentum vasculosum* of Deiters (14), which corresponds to the stria vascularis of Mammals. In Birds, too, the epithelium of the tegmentum displays many peculiarities. According to Deiters—whose statements I can confirm—there are found inserted, as it were, among the transparent cubical cells, nucleated, darkly granular bodies, of a pretty uniform size, whose cell-protoplasm has a "felt-like" character. A clear narrow piece, with three or four irregular sides, and carrying, as I have sometimes found, small hairs, rises out from the free surface of the felt-like cell body. The opposite end terminates in a short point (fig. 424, *E*).

The *sulcus spiralis externus* is found in Mammals to be lined with a very distinct cylindrical epithelium; the layer beneath it consists in Adults of a homogeneous tissue, clear like glass, which passes continuously into the triangular prominence of the *ligamentum spirale*, and from there into the homogeneous layer of the membrana basilaris.* Boettcher (4), as I see from the report of Schweigger-Seidel (Virchow's und Hirsch's Jahresbericht für 1868), has recently revived Todd-Bowman's (54) view—long ago disproved by Kölliker (32)—that the ligamentum spirale contains smooth muscular fibres. My own investigations, which have been numerous, confirm the statements of Kölliker.

The *crista spiralis* has offered not a few difficulties to those who have

* There is no unanimity among authors as to what should be understood by the expression ligamentum spirale. Kölliker, who introduced the name, and Löwenberg also apply it to the entire semilunar connective-tissue cushion, which unites the outer wall of the ductus cochlearis to the cochleal incasement. In the different species of animals it varies considerably in form and size, at one time encroaching very much on the scala tympani, especially in the lower turn of the cochlea, and at another time not doing so (see figs. 408 and 409). I myself prefer to apply the name—as Henle also appears to have done—only to that prominent, in Adults homogeneous, portion of the cushion which in transverse sections appears triangular in shape, which passes continuously into the membrana basilaris, and which in reality corresponds to a ligament.

hitherto busied themselves with the anatomy of the cochlea. These difficulties, I think, may be accounted for in part by the extraordinary shape of the elements which are found here, but especially by the peculiar manner in which the two principal types of tissue—the connective substance and the epithelium—are combined. Nowhere else in the organism are these two types similarly combined.

In a vertical section through the axis (figs. 408 and 409) the crista appears like a hook-shaped thickening of the lamina spiralis ossea, attached to it on its vestibular side. There is no sharp line of separation between it and the bone; the stellate cells of the latter are met with again in the basis substance of the crista, and vascular loops also project into it. In addition, lime salts are found deposited in it in the form of small irregular scales, while in Bats ossification seems to take place as a pretty regular thing. Usually, however, the basis substance of the crista appears to be composed either of stiff fibres or of a more homogeneous substance, and manifests the same behavior toward reagents as would a dense connective substance. Hence I believe it can most correctly be interpreted as an "osteogenic substance" (in the sense given to it by H. Müller and Virchow) which is developed in connection with the vestibular periosteum of the lamina spiralis ossea. I might mention here in passing that, when treated with perosmic acid or the chloride of palladium, the crista takes on a somewhat deeper color than the subjacent bone.

If we look at the crista from the vestibular side (figs. 411 and 412), the projecting edge appears to be subdivided by deep furrows into individual portions of nearly the same size and like oblong quadrangles in shape—Huschke's (28) *auditory teeth*, which in point of fact resemble a row of incisor teeth seen from in front. To the inner side these teeth pass into a number of round or oblong structures (fig. 412 *d*) which often appear of a peculiar brilliancy, and represent nothing more nor less than projections of the osteogenic substance of the crista. The furrows separating these structures as well as those lying between the auditory teeth are filled with small round and angular cells, which belong undoubtedly to the epithelium of the ductus cochlearis—a view shared also by Kölliker, at least so far as a portion of them are concerned. Toward the outer side these cells are directly continuous, through the interdental furrows, with the epithelium of the sulcus spiralis internus (fig. 411); then, on the other hand, they pass round uninterruptedly into the tympanal epithelium of Reissner's membrane (figs. 408 and 411). At the extreme margin of the teeth, as well as at the summit of the projections, the cells are wanting. In this locality the membrana tectoria (see farther on, and figs. 408 and 409 *M. t.*) rests directly upon the osteogenic substance of the crista; still even here a few flattened cell-rudiments are sometimes met with. The epithelial pathways, which lie between the teeth and the projections of the crista, run together on nearing the angle of attachment of Reissner's membrane, and finally unite to form a continuous layer (fig. 411 *e* and e_1). Mr. Baer (student of medicine), while making the drawings of these preparations, called my attention to the direct connection which exists between the cells we have just described and the ordinary epithelium lining the duct. The principal proof, however, of the correctness of this statement is to be found in the history of the development of these parts, for in embryos the duct possesses everywhere a continuous epithelial lining which is only apparently interrupted by the great development of the osteogenic substance of the crista, and also by the contact of the membrana tectoria; in reality, however, the continuity is maintained unbroken by way of

the interdental furrows. In this way it happens that in transverse sections we see the connection at one time, and at another fail—according to whether the section include a furrow or a tooth. The remarkable

Fig. 411.

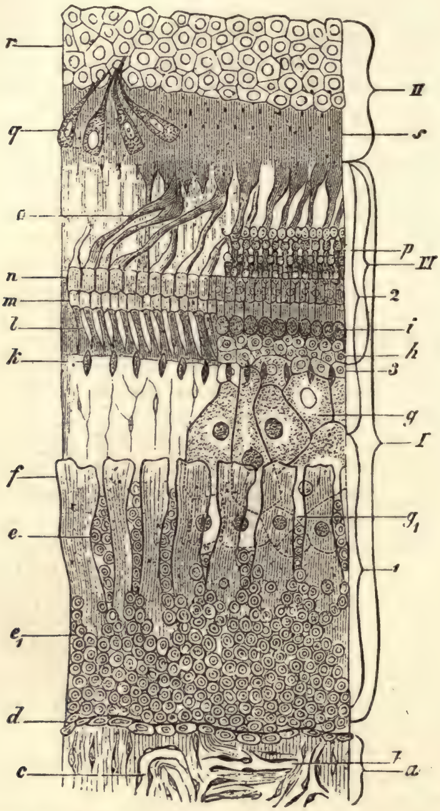

Fig. 411. Tympanal wall of the ductus cochlearis, from the Dog. Surface view from the side of the scala vestibuli, after the removal of Reissner's membrane. $\frac{200}{1}$. *I.* Zona denticulata Corti. *II.* Zona pectinata Todd-Bowman. 1. Habenula sulcata Corti. 2. Habenula denticulata Corti. 3. Habenula perforata Kölliker. *III.* Organ of Corti. *a*, portion of the lamina spiralis ossea (the epithelium is wanting); *b* and *c*, periosteal blood-vessels; *d*, line of attachment of Reissner's membrane; *e* and e_1, epithelium of the crista spiralis; *f*, auditory teeth, with the interdental furrows; *g*, g_1, large-celled (swollen) epithelium of the sulcus spiralis internus, over a certain extent shining through the auditory teeth; from the left side of the preparation they have been removed; *h* smaller epithelial cells near the inner slope of the organ of Corti; *k*, openings through which the nerves pass; *i*, inner hair cells; *l*, inner pillars; *m*, their heads; *o*, outer pillars; *n*, their heads; *p*, lamina reticularis; *q*, a few mutilated outer hair cells; *r*, outer epithelium of the ductus cochlearis (Claudius' cells of the authors); removed at *s* in order to show the points of attachment of the outer hair cells.

feature in the histology of this structure is the peculiar combination of epithelium with osteogenic substance; the latter has certainly never been observed anywhere else as the immediate substratum of a genuine epithelium.

The relations of the crista vary to an unusual degree in the different species of animals. The flattest, but at the same time the longest crista, is to be found—as Löwenberg (39) has rightly stated—in Man; the auditory teeth here project but little. Relatively the largest, and perhaps also the highest

Fig. 412.

Fig. 412. Crista spiralis after the removal of all the parts which cover it. From a Woman, æt. 28. Surface view from the vestibular side. $\frac{300}{1}$. *a*, labium tympanicum of the crista (where it passes into the membrana basilaris: bottom of the sulcus spiralis internus); *b*, *c*, auditory teeth of the labium vestibulare; beneath *c* is the sulcus spiralis internus, which is drawn in a foreshortened condition, embraced by both labia; *d*, *d*, projections of the crista; *e*, *e*, sections of small projections; *f*, *f*, furrows between the projections; toward *g* they gradually diminish in size until they attain the level of the lamina spiralis ossea; bone-cells shining through.

crista, with extremely sharp, almost claw-shaped teeth, is to be found in the Bat. It steadily diminishes both in height and size as it approaches the cupola of the cochlea. As to the physiological signification of this strange structure we cannot even form a conjecture, unless we assume that it serves as a support for the membrana tectoria.

After the removal of the epithelium in the neighborhood of the organ of Corti, the vestibular surface of the membrana basilaris appears either smooth, or, at all events, only feebly striated in the radial direction. The *vas spirale* with its bands of adventitial connective tissue may be seen shining through from the tympanal surface.

The vas spirale of Huschke (figs. 410 and 418), which is sometimes double, is a small vein embedded in the homogeneous basis substance of the membrana basilaris, after the fashion of a sinus duræ matris (fig. 418). It anastomoses with vessels of

the lamina spiralis ossea through radial branches (fig. 410) that are given off at regular intervals. Farther to the outside, the next vessel we meet with is at the root of the ligamentum spirale—an observation of Breschet's, which I have been able to corroborate in many instances (fig. 409).

Beyond the points of insertion of the outer pillars of Corti (see farther on) the membrana basilaris is distinctly striated in the radial direction [Zona pectinata of Todd-Bowman (54)]. The striæ constitute a thin cuticular lamella, which lies upon the vestibular side of the homogeneous connective-tissue substratum of the membrane and belongs to the epithelium of the ductus cochlearis. These relations can best be seen in vertical sections (fig. 418), in which three layers can be distinctly made out:* first the cuticular layer (*u*), whose striated appearance I consider, with Henle (26), to be due to the presence of delicate fibres; then the middle layer (*b*), composing the chief mass of the membrana basilaris,—a comparatively thick, structureless membrane, which passes continuously into the labium tympanicum of the crista spiralis (see fig. 408); finally, beneath the middle layer, on the tympanal surface, a stratum consisting of the most delicate fibrils of connective tissue which follow chiefly a spiral course and are interspersed with delicate spindle-cells (fig. 421), which of course appear round on cross-section, while the fibres look like a dotted granular mass. The younger the animals, the more feebly developed on the one hand will be the middle homogeneous layer, while on the other hand the tympanal fibrous layer will be thicker; the latter, moreover, is found, at least in Man, more fully developed in the first turn of the cochlea than elsewhere. These fibres of connective tissue are evidently the remains of the original mucoid tissue of the scalæ.

I would scarcely venture to express an opinion as to whether the membrana basilaris possesses a specially marked degree of elasticity or not; at all events it does not manifest any great tendency to roll up at the edges; nor is it difficult to tease apart. As may be learned from good transverse sections, the membrane is always stretched out smooth and straight between its two points of attachment.

The parts of the ductus cochlearis described thus far must be considered as constituting the connective-tissue wall proper of the ductus—membrana propria—to which I also reckon : Reissner's membrane, the innermost layer of the lateral connective-tissue cushion, together with the stria vascularis and ligamentum spiralis, the homogeneous layer of the membrana basilaris, and the crista spiralis. It is only in relation to the latter that doubts might be raised, and in regard to this point I would remark that in Man it is an easy matter, after the cochlea has been left for some time in glycerine, to separate the crista, with Reissner's membrane and the membrana basilaris attached, from the outer end of the lamina spiralis, and so to represent it as an integral portion of the wall proper of the ductus.

Epithelial Lining of the Ductus Cochlearis. Organ of Corti.

We have already described that portion of the cochleal epithelium which covers the crista spiralis, Reissner's membrane, and the external wall of the ductus; it still remains for us to describe the most important part—the epithelium of the membrana basilaris.

Kölliker's *organ of Corti* (figs. 408, 409 *f–p;* fig. 411 *III;* fig. 413) constitutes the central point of the basilar epithelial stratum; its individual parts are more or less modified cylindrical epithelial cells and cuticular formations. The organ of Corti proper (see the transverse sections, figs. 408 and

* See also the statements of Deiters (13) and Löwenberg (39).

418) is grouped symmetrically on both sides of a central structure—the *arches of Corti*—which at the same time serves as a supporting framework. These last arch over the membrana basilaris and consist each of an *inner* and an *outer pillar*. Next to the inner pillars come the row of *inner hair cells* (fig. 413,

Fig. 413.

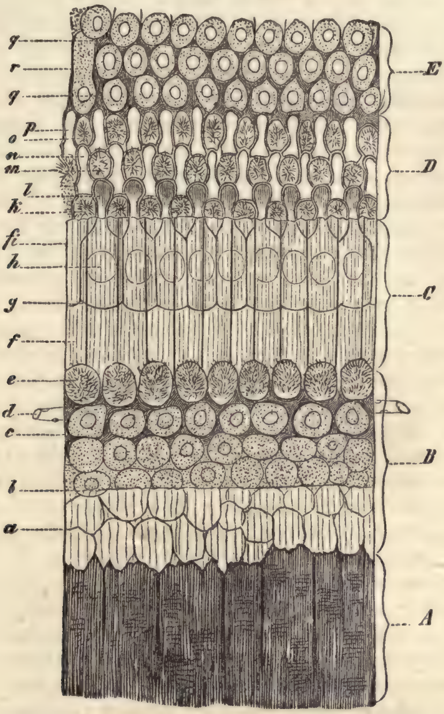

Fig. 413. The organ of Corti from the Dog; surface view from the vestibular side. $\frac{100}{1}$. Reissner's membrane and the membrana tectoria have been removed. *A*, Crista spiralis, whose dark color is due in part to the subjacent black nerve fibres (perosmic acid) which shine through. *B*, Epithelium of the sulcus spiralis internus. *C*, Heads of pillars. *D*, Lamina reticularis. *E*, Epithelium of the outer portion of the membrana basilaris.—*a*, Cells of the sulcus spiralis, which shine through from beneath the auditory teeth; *b*, outer margin of the auditory teeth (these last, owing to the fact that the instrument is focused to a deeper level, are scarcely perceptible); *c*, cuticular meshwork between the inner epithelial cells; *d*, location of the vas spirale; *e*, inner hair cells; *f*, heads of inner pillars; *fi*, head-plates of the inner pillars. The contiguous head-plates, when the instrument is focussed to a higher level, form above the heads of the outer pillars a clear cuticular roof, which extends from the inner to the outer hair cells. *g*, line of separation between the outer and inner pillars; *h*, heads of the outer pillars shining through the head-plates of the inner pillars. Within each head may be seen a bright circle—the optical transverse section of the body of the outer pillar, which shines through. *l*, phalangiform head-plates of the outer pillars (first phalanges); *k*, first rings with the tufts of hair of the first row of outer hair cells; *m* and *o*, second and third rings and tufts of hair; *n* and *p*, second and third phalanges; *r*, prop-cells of Hensen; *q*, cuticular meshwork between the epithelial cells (Deiter's terminal frames (Schlussrahmen)).

e, and fig. 418, *i*), the *granular layer* (fig. 418, *h–i*), and then, beyond, the epithelium of the sulcus spiralis internus. The cells of the latter grow

steadily higher from the deepest recess of the sulcus to the hair cells ;* the hair cells themselves reach to the summit of the arch, so that this inner portion of the organ of Corti forms a slope extending inwards from the arch.

The outer portion of the organ of Corti, which is somewhat broader and in many animals more or less steep, slopes outwards. It consists of the three rows of *outer hair cells* and of the immediately adjoining cylindrical epithelial cells, Hensen's *prop-cells*, which grow shorter and shorter until they pass into the simple cubical epithelium of the zona pectinata.

To this complex arrangement of cells are still to be added two membranous cuticular structures, the *membrana tectoria* (*M. t.* figs. 408 and 409), and the *lamina reticularis* (l–l_1, fig. 418, *D*, fig. 413—surface view).

The pillars of Corti possess, when seen in profile, the form of a slender Roman S (like the integral sign employed in calculus). The upper enlargement of the letter answers to the "head," the lower to the "foot," and the staff-shaped portion, uniting the two, to the "body" of the pillar. There are also attached to the head special plate-like processes—the "head-plates." The inner pillars possess two of these plates, which, however, pass continuously into each other : on the inner side a small one, which in profile appears almost like a hook (fig. 414 *Bg*) while seen in front, from the outer side it shines through like a dark ridge ; on the outer side a large one, which is bent in varying degree and represents the plate-like continuation of the body. This outer plate is bent over the head-piece like a hood, and shows sometimes, in Vesperugo, for instance (fig. 414 *D*), a distinct hollowing out of the external surface. The head-piece of the inner pillar projects outwards like a solid triangle with a rather blunt apex (fig. 414 *C*, *D*) ; its upper (vestibular) borders are slightly curved and the side margins are also somewhat concave.

The basilar surface of the inner pillars is nearly rectangular in form ; in profile the pedestal appears triangular. The pedestal of the outer pillars is considerably larger, and spreads itself out like a fan over the membrana basilaris. The body is more slender and the double curve of the S stands out in a more pronounced manner. The head faces inwards, in the opposite direction to that of the heads of the inner pillars, and presents in profile the appearance of a portion of a sector, somewhat similar to the form presented by the profile aspect of the caput astragali.

The head of the outer pillar can best be compared with the caput astragali ; here, however, both side surfaces—which correspond to the malleolar articular surfaces of the talus—are equally large, and the upper surface is not hollowed out, but is uniformly convex. Deiters (13) compares it to a capsized skiff, Löwenberg (39) to a Bird's head, whose beak would then correspond to the head-plate. For the inner pillar, the upper end of the ulna will afford us the necessary points for comparison. The processus coronoideus resembles the triangular projection (already described) of the head of the pillar ; if we imagine the olecranon somewhat lengthened anteriorly and bent over, it will then be found to correspond accurately to the outer head-plate, while the dorsal tuberositas olecrani would answer to the hook *g* (fig. 414, *B*) ; the lateral fluting too would find its representative in the sinus lunatus ulnæ.

The head-plate of the outer pillar arises by a long neck-piece from the middle of its external upper border, and passes into an oar-shaped enlargement (fig. 414, *A*, *d*) ; it constitutes, as will be seen farther on, the first phalanx of the lamina reticularis.

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* In the full-grown Mammal the epithelial lining never fills up the sulcus (in embryos it occasionally fills it, according to Kölliker and Hensen), but always remains as a single layer up to the region of the inner hair cells (Hensen).

It is a remarkable fact that in each of the two pillars a finely granular cell-protoplasm is to be found in two spots, in the head and in the pedestal. In the last-named situation (fig. 414, *B* *c* and γ; fig. 418, *n* and *o*) this formation was to a certain extent known even to Corti. It represents a nucleated, variously-shaped mass of protoplasm, which is firmly united with the substance of the pillar, and, as we learn from the embryology of these parts, simply constitutes the nucleated remains of one of the cells from which the pillars are formed. In the profile view these cell-remains are found impri-

Fig. 414.

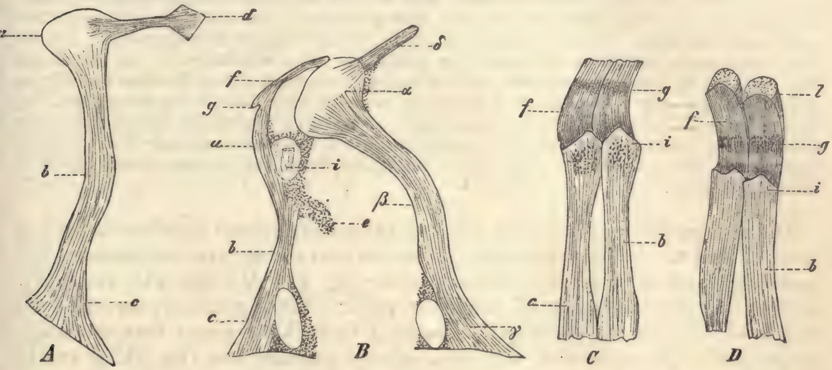

Fig. 414. Isolated pillars. $\frac{800}{1}$. In all the figures *a* (or α) indicates the head, *b* (or β) the body, and *c* (or γ) the pedestal of the pillar. *A*, outer pillar, from Mus musculus. Head seen somewhat in front and from above; head-plate with phalangiform end; *B*, inner and outer pillars in almost their natural position (profile view); from Mus musculus; *f*, head-plate of the inner, δ that of the outer pillar; *g*, inner hook-shaped process of the inner head-plate; *i*, head, with a clear portion resembling a nucleus, and granular protoplasmic remains; *e*, detached portion of protoplasm; *c*, nucleus with protoplasmic remains—in the pedestal; *C*, outer surface of two inner pillars seen from the front; from Mus musculus. Same lettering as in *B*, *D*. Two inner pillars from Vesperugo noctula, also seen from in front. $\frac{600}{1}$. The head-plate shows a distinct groove-shaped excavation, and at *l* a finely dotted appearance; the rest of the lettering is the same as before.

soned in the acute angle which every pillar forms with the membrana basilaris. It is a very frequent thing, as Boettcher was the first to state [see also in Hensen (27)], to see the protoplasm stretching along the membrana basilaris from one pillar to the other (fig. 419, *h*). As the remains of these connecting bridges, we not unfrequently find threads lying upon the membrana basilaris between the pillars; these threads (Deiters' system of supporting fibres), however, must not be mistaken for nerve fibrils.

We know less about the protoplasmic remains on the heads of the pillars, and they seem to have received less attention.* In this locality they lie upon the outer side of both pillars, that is, in the case of the inner pillars at the summit of the arch (fig. 414, *B* *e*) immediately beneath the most

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* Hensen (27) states (page 499) that the protoplasm on the pedestals of the pillars extends up over the pillars to their very heads; minuter details, however, are wanting. Perhaps the plate-shaped appendages of the heads of the inner pillars—which Max Schultze (50) has described, and which project, it is said, into the space beneath the arch—owe their origin to these protoplasmic remains.

prominent portion of the head-piece, while in the case of the outer pillar they lie immediately beneath the point of origin of the neck-piece of the plate-like process. In young animals I have also sometimes seen a nucleus here, similar in size and form to that on the pedestal. After treatment with a 0.05 per cent. solution of chromic acid, there appears in the head of almost every pillar (see fig. 414, *B i*) a nucleus-like structure, while the surrounding mass presents a finely granular appearance and passes into the protoplasmic appendage just mentioned.

When hardening reagents are employed, the bodies and pedestals of both pillars display very distinct longitudinal striations, and we now and then succeed in seeing them break up into fine stiff fibres, which are continuous with the striated lamella of the membrana basilaris. The head-pieces, however, always remain homogeneous ; I have never observed a cavity in the bodies or pedestals. The substance of the pillars, as first noticed by Boettcher, shows itself to be very resistant; they dissolve quickly in caustic potash only ; in acids and solutions of salts they shrivel up somewhat; in Man I have found the pillars in a good state of preservation twenty-four hours after death. The great bulk of these formations should be classed among the cuticular structures ; the connection (soon to be described) with the lamina reticularis also favors this view.

In the formation of the arch the two pillars are joined together in such a manner that the head of the outer pillar fits into the excavation between the head-plate and the head of the inner pillar (fig. 414 *B*; figs. 418 and 419). In this way the head-plate of the inner pillar must of course cover the head and head-plate of the outer pillar, but still in such a manner that the much longer phalangiform end of the latter always remains free (fig. 413 *fi* and *l*; fig. 416 *c* and *d* ; fig. 421 e_1. Owing to the fact that the inner pillars are more numerous, and their heads correspondingly smaller, the head of an outer pillar will always be found to rest on the heads of at least two inner pillars, which accounts for the aforementioned lateral grooves in the heads of the inner pillars. By this circumstance the consolidation of the pillars is rendered very firm. The inequality as to number in the two sets of pillars produces a similar condition of things to that found in the ginglymus of the elbow-joint : lateral displacements of the pillars are thereby rendered impossible. It is still an open question, however, whether a radial (about a spinal axis) joint motion may not exist between the heads of the pillars. The contiguous surfaces, whenever observed, always appeared smooth to me. The pillars, especially the outer ones, are so firmly attached to the membrana basilaris that oftentimes the bodies will break, while the pedestals retain their attachments; hence a motion like that just described could only take place during the actual bending of the pillars.

If we bear in mind the kind of union that exists between the heads of the pillars, we shall be able to understand the somewhat complicated picture presented by the organ of Corti when looked at from the vestibular side (figs. 413 and 421). Here are displayed a number of spiral and radial lines, the former of which (the spiral) are due in the first place to the inner and outer boundary-lines of the heads of both pillars, and in the next place to the outer boundary-line of the head-plates of the inner pillars (see fig. 421), while the latter (the radial) are due to the boundary-lines between the head-plates of the individual inner pillars, and to the head-pieces and neck-pieces of head-plates of the outer pillars, which may be seen shining through. In regard to this point I would refer the reader to the explanation of figs. 413 and 421, which he may combine with the pictures of vertical sections presented in figs. 418 and 419. I would like to add a few explanatory remarks in relation to the inner boundary-line of the head-plates

of the inner pillars. Between every two inner hair cells (see fig. 413) this head-plate projects almost in the form of a phalanx. The inner hair cells are much broader than the inner pillars, and for every hair cell there is a round place cut out from the substance surrounding the head-plates, so that each individual head-plate—one of which belongs to every inner pillar—must possess a different shape, according to whether the pillar stands directly opposite a hair cell or between two of them. Thus it happens that in isolating the inner pillars we find their inner appendages of varying form, although as a general thing they appear, as already stated, like a small hook when seen in profile [See Deiters' careful description (13)].

By their union the pillars bridge over a sort of tunnel, which is continued in a spiral direction through the entire length of the lamina spiralis, almost to the end of the hamulus. The transverse section of the tunnel shows it to possess a triangular lumen,* whose longest side as a rule is the membrana basilaris, the shortest the inner pillar. The smaller the species of animal, and consequently the narrower as a general thing the membrana basilaris, the shorter are the pillars, the steeper is their inclination to the membrana basilaris, and the higher, comparatively speaking, is the arch; then also the difference in size between the outer and inner pillars disappears almost entirely. Very long pillars with a large span belong to the larger animals; in the Human being the arch is at the same time the flattest, resembling when seen in transverse section a low trapezium (see, *e.g.*, fig. 408 (Man) and fig. 409 (Vesperugo)). Other peculiarities are to be found in the forms of the pillars. They are short and compact in the Chiroptera and Mice; in Man, the Dog, and the Ox, they are slender and very much bent. The longest head-plates exist in Man. In the different parts moreover of the lamina spiralis, differences are found in the size of the pillars, and in the height and span of the arch. As a rule these dimensions decrease as we approach the hamulus. For further and more accurate information on this point, see Hensen (27).

The most important structures resting upon the inner slope of the arch of Corti are the single spiral row of *inner hair cells* (fig. 418 *i*, figs. 421, 422, and 423). They are of a compact conical shape: the large nucleus lies pretty nearly in the middle of the very delicate cell body. The latter passes on the tympanal side into a long process, which becomes lost in a layer of small cells—the *granular layer* (fig. 422). The vestibular extremity of the hair cells is embraced by the plate-like appendages of the heads of the inner pillars (fig. 420, *i*, *h*), and it carries upon the cuticular cover a close crop of strong staff-shaped hairs, which appear to be very resistant structures. The epithelial cells of the sulcus spiralis which lie next to the hair cells are cylindrical in shape and alternate in position with the hair cells (figs. 413 and 418). They cover over the granular layer spoken of above.

More obscure are the relations of the cells that lie on the outer side of the arch, of which the hair cells—Corti's cells of the authors—are among the most difficult objects of study in the cochlea. In describing them I shall follow the statements made by Gottstein in 1869 at the convention of naturalists in Innsbruck. The *outer hair cells* stand in three (or four) parallel contiguous rows, which pursue a spiral course. The individual cells

* It is quite proper to speak of a *lumen* here, for, apart from the protoplasmic remains of which we have already spoken as being attached to the pillars, from Deiters' bands of supporting fibres along the bottom of the arch, and from the nerve fibres which pass through the tunnel, there is nothing to be found in it besides the endolymph. (See also Reichert (44).)

of each row alternate very regularly in position with those of the next row (fig. 413). In each row there are about the same number of cells as there are outer pillars. According to Gottstein's account the cells possess each two nuclei, an upper smaller, and a second situated near the lower

Fig. 415.

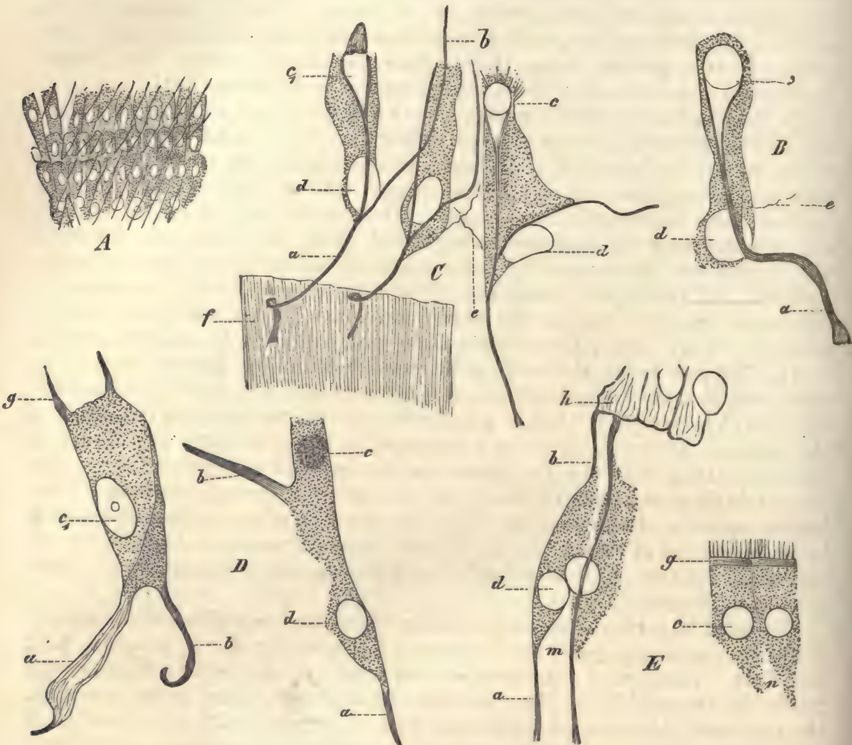

Fig. 415. *A*, the three rows of outer hair cells in situ (after the removal of the lamina reticularis and the membrana basilaris) together with the phalangeal and basilar processes; from the Dog (chloride of gold preparation). $\frac{300}{1}$. *B*, outer hair cell (twin cell) from Vesperugo noctula. $\frac{800}{1}$. *a*, basilar process (the phalangeal process invisible); *c*, upper nucleus with prolongation; *d*, lower nucleus; *e*, delicate thread (nerve ?); *C*, three outer hair cells from Vesperugo noctula, in connection with the basilar membrane; *a*, *d*, *c*, and *e*, the same as in *B*. At *c* the delicate fine hairs are still preserved; at c_1 the nucleus is wanting, while from above there rises a conical projection—probably a portion of protoplasm; *b*, phalangeal process; *f*, fragment of the basilar membrane; *D*, two outer hair cells from Man (Girl, æt. 23). $\frac{800}{1}$. Same lettering as before. *c*, darker spot: whether or not a nucleus I was unable to decide; c_1, upper nucleus with nucleolus—which in the hair cells are always remarkably small; the phalangeal process *b* of this cell has been torn off and the remnant is folded over toward the basilar membrane; *E*, separate twin cells, from the Dog. $\frac{800}{1}$. Both sets of cells, *m* and *n*, were directly connected together in the first place, the sharp end at *n* passing continuously into the cell-protoplasm of *m*, and the hairs being directed upwards; the phalangeal processes *b* are still connected with the phalanges (*h*); *g*, cuticular frames of the rings, surmounted by hairs; *a*, *c*, and *d* as before.

end of the cell. Near the lower nucleus two large processes are given off from the body of the cell, the elongated *basilar process*, which is firmly

attached to the membrana basilaris by means of a small triangular swelling (fig. 415), and is the longer and larger of the two; and the phalangeal process, which is narrower, pursues a somewhat crooked course, and becomes fused with one of the phalanges of the lamina reticularis which lie just beyond (externally) and to one side of it (Gottstein). It is not a rare circumstance moreover to find delicate short threads—nerve processes (fig. 415)—hanging from the body of the cell.

The basilar process runs straight up along the body of the cell and then divides into two arms, which like the blades of a forceps enclose the upper nucleus (fig. 415, *B* and *C*). Looking down upon the surface, after the hairs of the cell have fallen out, we can see these arms shining through from below, and the semicircular areas which they enclose will appear to lie within the rings of the lamina reticularis, into which the upper (vestibular) end of the cells is inserted. Deiters (13) was the first to observe this area, but he did not comprehend it correctly, although he was already familiar with the arms enclosing the nucleus. Kölliker (30) seems to have mistaken it for the surface view presented by the cilia, for (l. c. fig. 521) in exactly the same position where the arms shine through he has drawn a semicircular line and explained it as a wreath of cilia. As in the case of the inner hair cells, so here, the cilia form a thick tuft upon the entire end-surface of the cells (Middendorp (40); figs. 413 and 416).

A closer examination of the outer hair cells reveals the fact that they are composed of two-tailed cells which have become fused together—true twin-cells or double cells. One of these cells turns its hairy nuclear end upwards and is attached by its tail to the membrana basilaris; the other winds round the first in a spiral direction and is firmly adherent to it, the nuclear end being turned downwards (toward the scala tympani) while the tail (phalangeal process) runs upwards. From the fusion of the two conical cells results the two-tailed and double-nucleated double body just described (fig. 415, *B*, *C*, *D*; fig. 418, *p*). The fusion of the two cells into a single mass varies in completeness in the different animals. In the Rodentia and Chiroptera it is almost impossible to separate the two cells from each other without injuring them to a great extent and rendering the fragments irrecognizable. In Dogs (fig. 415, *E*) I have succeeded a few times in separating a somewhat mutilated ciliated portion from the basilar process and the rest of the cell-body, which then will be seen, as represented in the figure, provided with two tails; these two-tailed remains have been described by Deiters (13) as special cells, under the name of "hair cells" ("Deiters' cells," Kölliker). As in the case of the inner hair cells, so here also the upper end of the cell carries a thick cuticular lid, which fits into the ring of the lamina reticularis and carries cilia.

The outer slope of the organ of Corti shows many variations, according to the species and kind of animal. It is a remarkable circumstance that the Human being possesses *four* or even *five* rows of outer hair cells (figs. 416 and 421), while in all the animals I examined there were always only three rows*.

In Man, furthermore, the hair cells are very large, the processes thick and more like ordinary cell-protoplasm, and the hairs very long and stiff, like

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* Hensen (27) states—in a passing remark, and without mentioning whether in animals or in Man—that in the second and third turn "more than four hair cells" appeared to be present. Löwenberg, in a drawing (fig. 4) of a transverse section of the organ of Corti from a Child, has represented four tufts of cilia, but he makes no mention, either in the text or in the explanation of the figure, of four rows of hair cells in Man

bristles. In the embryo we find in the place of the hair cells a closely packed group of cylinder cells, which gradually grow flatter until they become merged in the epithelium of the zona pectinata. Probably each hair cell originates from the subdivision of a cylinder cell, and both products of the subdivision remain more or less firmly united to each other.

Besides the bands of spiral fibres—which we shall mention later, when treating of the nerves — there are no other elements to be seen among the hair cells. In regard to the cylindrical prop-cells of Hensen (Fig. 416, *h*), which follow next in order on the outer side of the hair cells, what has already been said on page 1028 will suffice.

Another peculiarity requiring special mention is the occurrence of numerous light-brown pigment granules, which are found, especially in Man, in the plates of the lamina reticularis, and in the epithelium of the ductus cochlearis, particularly in the stria vascularis; Corti (10) has also called attention to these granules (page 111).

The *membrana tectoria* of Claudius (Corti's membrane, Kölliker) (figs. 408 and 409, *Mt*) begins, in the immediate neighborhood of the line of attachment of Reissner's membrane along the crista spiralis, as an immeasurably fine lamina, which covers and is firmly adherent to the crista; from this point it at once increases very considerably in thickness, attaining its greatest thickness in the sulcus spiralis internus, and ends, according to my experience,—which is the same as Hensen's and Gottstein's,—in a very delicate, thin free margin, in the neighborhood of the outermost hair cells. It lies immediately upon the surface of the organ of Corti—that is, upon the lamina reticularis—throughout its entire extent.

The chief substance of the membrana tectoria appears finely fibrillated in a radial direction. Where the membrane lies upon the crista, its under surface presents the appearance of an irregularly shaped network (relief of the crista); its terminal portion likewise presents a delicate retiform design, which in all probability is due to the imprint of the prominent tufts of cilia of the outer hair cells (see in particular the description of Löwenberg (39) and Henle (26)). A subdivision of this membrane into zones is surely an unnecessary burden for the organ of Corti, which is already so abundantly laden with names. The consistence, however, of the membrana tectoria is a matter of particular interest. I do not know how it came to have the reputation of being an unusually elastic membrane; portions of it isolated, in a fresh condition, are found to be quite soft and may be folded into any shape; the edges are never found rolled up. When hardened in alcohol the membrane becomes very much contracted, and retains on its surface the impression of the structures which may have happened to be in contact with it. Occasionally I have found the tufts of cilia of the outer hair cells sticking in the substance of the membrane; at the same time the latter had become somewhat displaced and had carried with it the lamina reticularis, together with the hair cells—all attached to the membrane by the tufts of hairs. These are not unimportant points, and I shall return to them farther on. For the present it will be sufficient to show—as Hensen (27) alone, so far as I am aware, has shown—that the membrane of Corti possesses a pretty soft, almost gelatinous consistency. According to Kölliker (30, 34) and Hensen (27) it should be considered as probably a cuticular formation (secretion) proceeding from the epithelial cells of the crista and sulcus spiralis internus. In embryos these cells constitute a thick layer, which subsequently shrinks away in the same proportion as Corti's membrane grows. In Birds, according to Hasse's (20) statements, the membrana tectoria passes without any sharp limits into the mucoid mass in which the otoliths of the lagena are embedded.

The most complicated structure of the ductus cochlearis is, beyond all question, the *lamina reticularis* (Kölliker), whose highly ornamental surface as seen from above is represented in figs. 413 and 421. The retiform lamella consists of a number of frames, resembling rings and lady-fingers (or digital phalanges) in shape—Boettcher's (2) *rings* and Deiters' (12) *phalanges*. The borders of these frames have double outlines, and it is possible to obtain isolated specimens both of the rings and of the phalanges. On the inner side of the arch of Corti [see the description of Deiters (13)] we find but a *single* row of phalanges and rings (see fig. 420, taken in part from a preparation of Gottstein's), from the latter of which the cilia of the inner hair-cells project. These rings are continuous with a second, incompletely reticular structure, which embraces the heads of the epithelial cells of the sulcus spiralis internus which are next in order. On the outer side of the arch of Corti follows the larger portion of the retiform lamella, composed of three or four rows of phalanges and rings, which correspond in number to the outer hair-cells. At the outer limit of the organ of Corti these phalanges and rings pass continuously into an irregularly-shaped cuticular meshwork—Deiters' terminal frames—which is constructed over the vestibular surface of the epithelium of the zona pectinata and of Hensen's prop-cells, and requires no special description in this place.

Fig. 416.

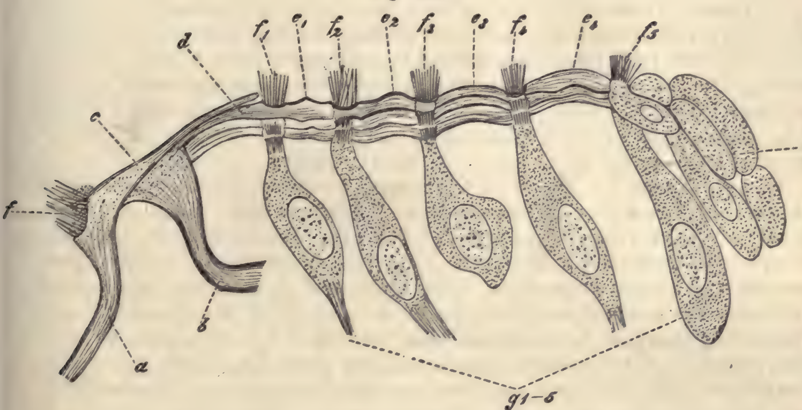

Fig. 416. Fragment of the lamina reticularis from the newly-born Child. Profile view. $\frac{800}{1}$. *a*, inner, *b*, outer pillar; only the head-ends preserved; *c*, head-plate of the inner pillar, terminating in front of the first tuft of hair, f_1; *d*, head-plate of the outer pillar with its phalangiform appendage, e_1; *f*, hairs of the inner hair-cells—the cells themselves have not been preserved; f_1-f_5, five tufts of hair belonging to the outer hair-cells, and projecting through the rings of the lamina reticularis (in surface views only four rows of hair-tufts could be counted with certainty; only here and there was a tuft found belonging to the fifth row); $e_1—e_4$, phalanges; $g_1—g_5$, mutilated outer hair-cells, still attached to the lamina reticularis; *h*, prop-cells (Hensen).

The rings and phalanges are so arranged as to alternate with each other in regular succession: a phalanx is always surrounded by four rings, and *vice versâ* * (a glance at fig. 413 will illustrate this point with sufficient

* Strictly speaking, this statement is true only when the head-plates of the pillars and the terminal frames are counted in, for otherwise in Man we could only say it of the rings of the third row, that on all sides they were surrounded by phalanges.

clearness). The first row of outer rings begins close to the outer end of the head-plates of the inner pillars; each phalanx of the second row forms the lateral boundary outwardly of the phalangiform end-piece of the outer head-plates (fig. 413, *k*, *fi*, *l*, *n*). In regard to the boundaries of the third ring, the only point to be noticed is that on the outer side (see fig. 413) completely formed phalanges are wanting, and in their stead we find Deiters' terminal frames.

Each ring encircles closely the basilar margin of its appropriate hair cell; the frame of the ring passes continuously into the frames of the contiguous phalanges, so that in isolating either one of them we always carry away portions of the others bordering upon it, in precisely the same manner as in a net we cannot remove one mesh without at the same time destroying the neighboring meshes. The frames of the phalanges being filled with a delicate membrane, these also become destroyed by the manipulation, leaving nothing behind but the simple framework.

The descriptions hitherto have been limited, like the above, to the external form of the lamina reticularis—we except of course the correct interpretation which Kölliker has already given to it, of being a cuticular covering-plate for the organ of Corti. To understand this structure, which at first sight appears so complicated, and to do fuller justice to the arch and organ of Corti, it is necessary that we should first consider all these parts in their proper connection.

In passing from within outwards in the organ of Corti—for the sake of simplicity we overlook the fact that in Man the hair cells are more numerous—we shall find, placed one behind the other, six rows of cells, which are arranged, so to speak, in alternating groups: the inner hair cells, the inner and outer pillars of Corti, and the three rows of outer hair cells. The regular alternation in their position is disturbed only by the difference in number between the inner hair cells and the pillars.

If we examine the pillars of Corti more carefully, we shall soon see that in their structure they correspond to an outer hair cell. Each pillar is to a great extent a cuticular metamorphosis of a double cell, one portion of which—the nucleated basis—rests upon the membrana basilaris, the other against the lamina reticularis. The nucleated part of this latter portion lies upon the head-piece of the pillars (the nucleated protoplasmic remains composing this part have already been described by us on page 1029); in the pedestals of the pillars these nucleated parts have been known for a long time past. The two processes are also not wanting. The basilar process belongs to the upper protoplasmic remains, that is, to the upper cell, and constitutes a part (the outermost periphery) of the body of the pillar; the phalangeal process is represented beyond a doubt by the head-plate; it belongs to the protoplasmic remains of the pedestal of the pillar (the under cell) and is united—in exactly the same manner as in the hair cells—so as to form one with the basilar process, that is, here, with the body of the pillar. The relations can be seen most distinctly in the outer pillars, but they can also scarcely fail of recognition in the inner. The development of the pillars, which was first studied by Kölliker, teaches that originally these structures are conical epithelial cells of the basilar membrane. That they are the product of the fusion of two cells is to be inferred from the demonstration of protoplasmic remains both in the head and in the pedestal—a nucleus being sometimes present in each of the protoplasmic collections. At the present time, however, I am unable to decide whether each pillar is the result of the fusion of two originally separate cells—as I believe to be the case in the outer hair cells—or of the subdivision of a single

cell whose two products of subdivision afterwards undergo a cuticular transformation.*

Each of the outer hair cells corresponds—as may be inferred from the manner in which they slope outwards—to a ring, together with its adjoining phalanx, which is situated on the outer side of it. Each phalanx is the cuticular coat of mail of the hair cell which lies beneath it; the cell furthermore adheres to the phalanx like the body of a Turtle to its shell, and, like a Turtle, it stretches out its head towards its appropriate ring. Hence we can explain the fact that the outer phalanges grow shorter while the last ones appear simply like irregular terminal frames, by remembering that the outermost row of hair cells slopes less than the others. Long and very sloping hair cells (Cat, Ox, and Man) are found in conjunction with a broad lamina reticularis with long drawn out meshes; while steeply inclined, short hair cells (Chiroptera) accompany a narrow lamina reticularis with short and broad meshes.

Leaving out of consideration for the moment the various peculiarities of the inner hair cells, the apparently complicated structure of the organ of Corti will be found to follow a simple plan. Several rows of cylinder cells (double cells) are arranged one after the other in regular order upon a broad zone of the lamina spiralis and are held fast between two membranous (cuticular) boundaries (the lamina reticularis and the striated lamina of the membrana basilaris). Of these cylindrical double cells, two sets—the pillar cells—have also undergone to a great extent a cuticular transformation, for the purpose of establishing a firm supporting arch for the whole. The cuticular covering lamella starts from the head-pieces of the arch and is composed of the ends of the cells; toward both edges it gradually grows thinner and thinner, by the constantly diminishing amount of substance deposited upon the inner and outer epithelium. Deviations from this plan are afforded by the inner hair cells, which in the first place cannot be considered as double cells, and in the next, like the inner pillars, do not correspond in number to the outer hair cells. The inner pillars appear to be the middle point of the whole, inasmuch as in both directions, inwardly and outwardly, they contribute to the formation of the lamina reticularis.

Special attention should also be called to the careful manner in which the outer hair cells are attached; by means of their two processes and the head-piece they are held immovable, and at the same time tense, between the lamina reticularis and the basilar membrane. These cells, together with Corti's pillars, are a peculiarity of the Human and Mammalian cochlea; I shall return to the inner hair cells when I come to speak of the nerve terminations.

We have now constructed the apparatus towards which the terminal filaments of the N. acusticus direct their course, and in whose most essential parts—the inner and outer hair-cells—they find their actual termination. Before treating of these particular points, I shall make a few remarks on the relations of the main trunk of the auditory nerve.

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* The head-piece corresponds, according to the foregoing account, to that end of the hair cells which carries cilia. For a long time past Gottstein and I have entertained the view (based upon various observations) that rudiments of cilia actually do occur on the head-ends of the pillars (see for instance fig. 421). The fibrillated structure of the body of the pillar also points to the same conclusion.

Auditory Nerve and its Relations to the Organ of Corti.

According to the statements of Stieda (51–53), which I follow here in the main, the nervus acusticus arises by two roots in the medulla oblongata. One root is composed of delicate fibres, and its ganglionic nucleus of origin—Stieda's central acusticus-nucleus—consists of small ganglionic bodies, situated in the floor of the fossa rhomboidea.* The other root, which, according to Stieda, consists of remarkably thick axis-cylinders, thicker than can be found in any other nerve, arises from a special, large-celled ganglionic nucleus of origin in the crus cerebelli ad medullam oblongatam—Stieda's lateral acusticus-nucleus. Deiters (16) also describes this nucleus, and gives a drawing of it, but he does not recognize the fact that the acusticus originates in its ganglion cells. For further details and literary references, see Stieda, *loc. cit.* Very soon after leaving the medulla, the root with large fibres is provided, like the posterior roots of the spinal cord, with a small ganglion.

Both roots speedily become merged into a single trunk, whose primitive fibres, as Czermak (11) found, not unfrequently subdivide and give off branches, and are probably to be considered as fasciculi of primitive fibrils, with simply a medullary sheath (page 123 of this book, II. 2), inasmuch as no sheath of Schwann can be demonstrated in them. In the porus auditivus internus the trunk of the nerve divides into two branches—ramus vestibularis and ramus cochlearis. The former of these possesses here a small ganglion—*intumescentia ganglioformis Scarpæ*—and subdivides into the rami ampullares, the ramus utricularis, and the ramus sacculi. The very much larger ramus cochlearis gives off first a small bundle of fibres to the septum membranaceum utriculi et sacculi (Henle, 26) and to Reichert's (45) macula cribrosa quarta—a fact disputed, however, by Middendorp (40)—and then passes through the tractus spiralis foraminulentus direct to the first turn of the lamina spiralis, and straight into the modiolus, whence it is distributed to all the other turns of the lamina spiralis. Before the bundles of fibres, however, enter the lamina spiralis, all the branches traverse the ganglion spirale, which is situated in the canalis ganglionaris, at the commencement of the lamina spiralis. Probably a bipolar ganglionic sphere is interpolated here in the course of every nerve-fibre. Numerous ganglion cells are also found in the course of the main trunk of the nerve and in the ramus vestibularis, where they present the appearance of simple nucleated swellings of the axis cylinder. (See fig. 39 of this book.)

Beyond the ganglion the fibres are spread out in nearly one and the same plane between the tympanal and vestibular lamellæ, though much nearer to the former they still possess their ample medullary sheaths, and form numerous anastomoses and plexuses (fig. 417). We can make out here the anastomoses between the coarse and the fine bundles. In Man the latter (fig. 417 *b*) are very numerous just before their entrance into the ductus cochlearis; in a surface view this gives rise to the appearance of a delicate serrated line. The individual terminal bundles of the nerve now rapidly diminish in size by losing the greater part of their medullary sheaths, and then pass into the cavity of the ductus cochlearis through fine canals in the membrana basilaris.

The delicate and, as a general thing, round canals for the nerves are of an appreciable length in the upper cochleal turn, for in this locality they traverse the

* Fourth Ventricle.—TRANS.

membrana basilaris obliquely, a few of the pale fibres anastomosing on the way with their neighbors. In the lower turn, however, they traverse the membrane in a more nearly perpendicular direction, so that in a surface-view we see before us regular holes, which in Man are small, round, and near together; while in the Dog and other animals (fig. 411 *k*) they are elliptical in shape, and larger. Löwenberg gives a detailed description of them; see also Kölliker, *Mikrosk. Anatomie*, p. 751.

Fig. 417.

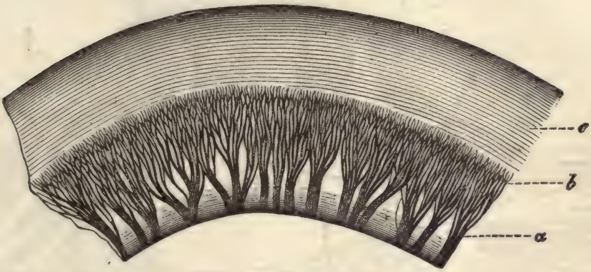

Fig. 417. Lamina spiralis of the first turn of the cochlea, seen from the tympanal side (1½ yr. old Child). Expansion of the N. cochlearis. *a*, large trunks with numerous anastomoses; *b*, girdle-shaped last row of delicate anastomoses; *c*, Membrana basilaris. $\frac{30}{1}$.

The pale fibres, after they have emerged from the openings, continue to pursue a radial direction in attaining their terminal organs. In correspondence with the inner and outer hair cells we must distinguish *inner* and *outer nerve terminal* fibres. Both the inner and the outer fibres, after their emergence, traverse first a scanty layer of round cells—the *granular layer* (fig. 418 and fig. 422)—which is situated between the inner slope of the organ of Corti, just where the nerve fibres emerge. Later, when I come to speak of the spiral bands of fibres in the organ of Corti, I shall return to the subject of this granular layer and its relations to the nerve fibres; for the present I shall accompany the radial nerve fibres to their points of termination.

The inner radial fibres pass—as I have often been able to prove (fig. 423)—directly through the granular layer and terminate in the pointed end of the inner hair cells. These fibres appear to me to possess a comparatively great breadth (1.5–2μ); I am therefore inclined to consider them, not as individual axis-fibrillæ, but as bundles of fibrillæ (axis-cylinders)—(see page 123 of this book). From their diameter they may perfectly well represent the undivided axis cylinders of the medullated acusticus fibres which enter the foramina nervina. Hasse (18–25) found that the termination of the nerves in the hair cells of Frogs and Birds was always similar to that described above (see farther on).

The outer radial fibres direct their course, as Gottstein has found, toward the tunnel of Corti, passing between the inner pillars and traversing the tunnel about midway between the summit and the base of the arch; in a profile view these fibres appear like stretched harp-strings. On leaving the arched space they pass through the outer pillars and direct their course—rising a little toward the scala vestibuli—straight to the outer hair cells, with which they become completely fused (figs. 418 and 419). In several preparations from the Dog and the Bat I have seen this termination of the nerves in the most convincing manner, at least so far as the innermost

row of the hair cells is concerned; as to the other rows, we may pretty confidently assert that the termination of the nerves is the same, for we can frequently see several fibres passing at the same time between the outer pillars.

Fig. 418.

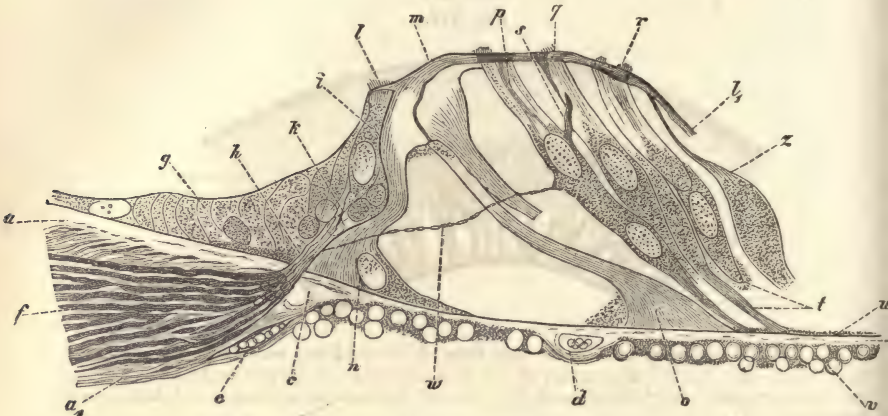

Fig. 418. Vertical section through the organ of Corti (Dog). $\frac{800}{1}$. *a–b*, homogeneous layer of the membrana basilaris; *u*, vestibular layer of the same, corresponding to the striæ of the zona pectinata; *v*, tympanal layer with nuclei, granular cell protoplasm, and transversely cut fibrils of connective tissue; *a*, labium tympanicum of the crista spiralis; a_1, prolongation of the tympanal periosteum of the lamina spiralis ossea; *c*, thickened commencing portion of the membrana basilaris, immediately to the outside of the point of emergence of the nerves, *h*; *d*, vas spirale; *e*, blood-vessel; *f*, bundle of nerves; *g*, epithelium of the sulcus spiralis internus (not well preserved); *i*, inner hair cell; *k*, its basilar process; in its neighborhood, just above the point of emergence of the nerves, are a few nuclei and a finely granular mass through which the nerve fibres radiate (granular layer); *l*, inner portion of the head-plate of the inner pillar and hairs of the inner hair cell; *m*, conjoined head-pieces of both pillars; the body here of the outer pillar has been cut through the middle; behind it are the body and pedestal *o* of the next pillar; *n*, pedestal of the inner pillar, with nucleated protoplasmic remains; *p*, *q*, *r*, three outer hair cells (only traces of the cilia preserved); the first one only is complete; of the other two only the head portions are visible; *t*, basilar portions of two other hair cells; *z*, Hensen's prop cell; l–l_1, lamina reticularis; *w*, nerve fibril, which is on its way to the first hair cell *p*, and may be followed through the archway back to the point of emergence of the nerves.

The outer radial fibres always appeared to me to be much more delicate than the inner. When fresh (figs. 419 and 420), they resemble most nearly the very delicate axis fibrillæ which are distributed to the rod-granules in the retina, as described by Max Schultze, and are characterized by peculiar drop-shaped varicosities. I have seen these fibrils very beautifully exhibited in an osmic acid preparation of Gottstein's. Max Schultze (50), as is well known, was also the first to describe similar pale nerve-fibrils in the cochlea, and I am inclined to look upon all these very delicate varicose fibrils that are found in the sulcus spiralis internus, by the side of the larger fibres which go to the inner hair cells, as radial fibres, even though they may appear (as in fig. 420) to be on their way to the inner hair cells (for both sets of fibres follow the same route up to this point). The same remark applies to the delicate fibres in fig. 422, which pass up through the granular layer and between the inner hair cells; for, as I have already stated, those

fibres which I positively saw terminating in the inner hair cells were much thicker. The varicosities of the outer radial fibres (see also fig. 28, p. 117 of this book) cannot be mistaken for anything else; after once seeing the genuine varicose nerve fibrils of the cochlea, one will not easily commit the error of mistaking connective-tissue fibrillæ for nerve fibrillæ. It is true that small granular swellings occur at pretty regular intervals here and there in the course of the extremely delicate connective-tissue fibrils of the tympanal surface of the basilar membrane, but they never possess the peculiar brilliancy and the exquisite drop-like shape of the genuine nerve varicosities.

Fig. 419.

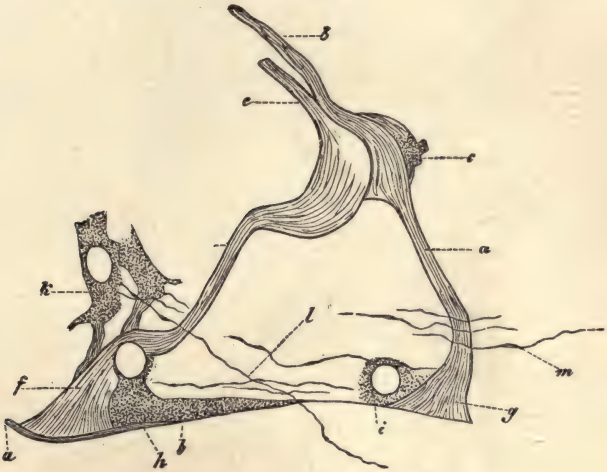

Fig. 419. Corti's arch, from Man (Maiden, aged 30). Teased preparation. $\frac{610}{1}$. (The natural position, as seen in sections, is not preserved.) *a*, inner pillar; *b*, its head-plate; *c*, attached fragment, probably from one of the inner hair cells; *d*, outer pillar; *e*, its head-piece (preserved only in part); *f*, its pedestal; *g*, pedestal of the inner pillar; *h*, nucleus with protoplasm extending over a large part of the distance between the two pillars; *i*, nucleus of the pedestal of the inner pillar; *k*, rudiments of two outer hair cells; *l*, *m*, disconnected portions of radial fibrils, which are distinctly varicose in character, and which—some of them at least—may be followed as far as to the outer hair cells (nerve fibrils).

Taking into consideration these two peculiarities and the circumstance that the drops are tinged black in perosmic acid, I would venture to interpret the genuine nerve varicosities as extremely delicate medullary sheaths. (According to this view, then, the medullary sheath would not be wanting even in Max Schultze's primitive fibrillæ—my axis fibrillæ.) Hasse, however, denies the existence of a medullary sheath even in the larger terminal nerve fibrils of Birds and Frogs; at the same time he describes them as still having a delicate sheath of Schwann after their entrance into the ductus cochlearis. Neither in Birds nor in Mammals have I ever made any observations that would favor such a view.

From the numerous specimens prepared by Gottstein and myself, I think I am justified in placing it as a fixed fact, in our stock of knowledge concerning the cochlea, that the radial fibres described above are nervous in character, and terminate in the inner and outer hair cells. I am convinced that no one who works with good methods will dispute these facts. The

question, however, still remains to be answered, whether other elements of a nervous character do not occur in the cochlea—I refer to the *spiral bands of fibres* discovered by Max Schultze.

Fig 420.

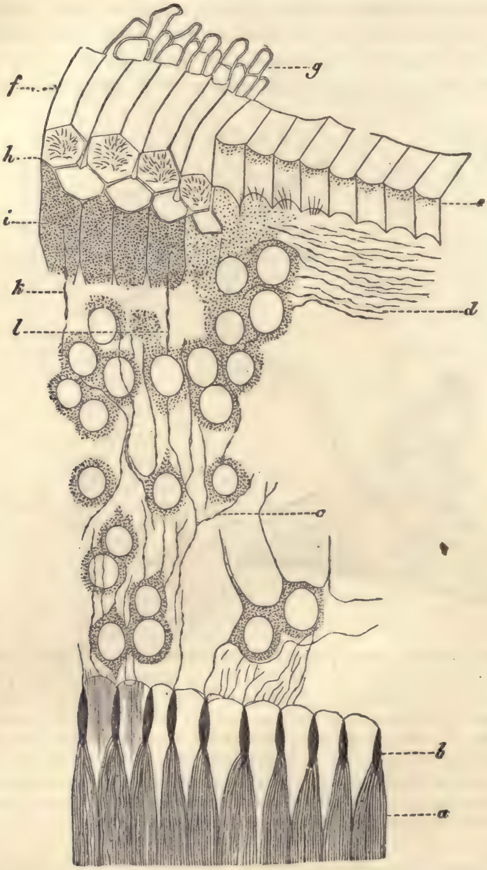

Fig. 420. Lamina granulosa acustica of the Dog, with the neighboring parts; the drawing corresponds to two preparations, one of which includes the region from *f* to *t*. The commencing portion of the arch of Corti, together with the inner hair cells, has been pushed very much to the outside of its normal position, and the granular layer has been lacerated in places. $\frac{610}{1}$. *a*, bundle of nerves (diagrammatic); *b*, foramina nervina; *c*, granular cells with processes and intervening delicate fibrillæ, some of which may be followed to the foramina nervina; *d*, group of spiral fibres, some of which are, as it appears, prolongations from the radial fibres which have bent round the inner hair cells; *e*, head-pieces of the inner pillars; *g*, commencing portion of the lamina reticularis; *h*, hairs of the inner hair cells *i*; *f*, head-piates of the inner pillars; *k*, *l*, distinctly varicose nerve fibrillæ, which pass out of view near the summit of the inner hair cells.

According to my observations, two principal sets of spiral fibres may be distinguished in the organ of Corti—the *inner* and the *outer band.* The inner and at the same time smallest band (fig. 421 *i*, fig. 422 *c*) corresponds to

the row of inner hair cells: it passes along the lower portion of these cells, beneath the lamina reticularis. The outer band consists in reality of three parallel subdivisions, which follow the three rows of outer hair cells, running in the spaces between the rows, at the same level as the inner band. The innermost subdivision runs between the row of outer pillars and the first row of hair cells; the other two subdivisions run in the interspaces of the following rows. In Man (fig. 421) I have thus far seen but three sub-

Fig. 421.

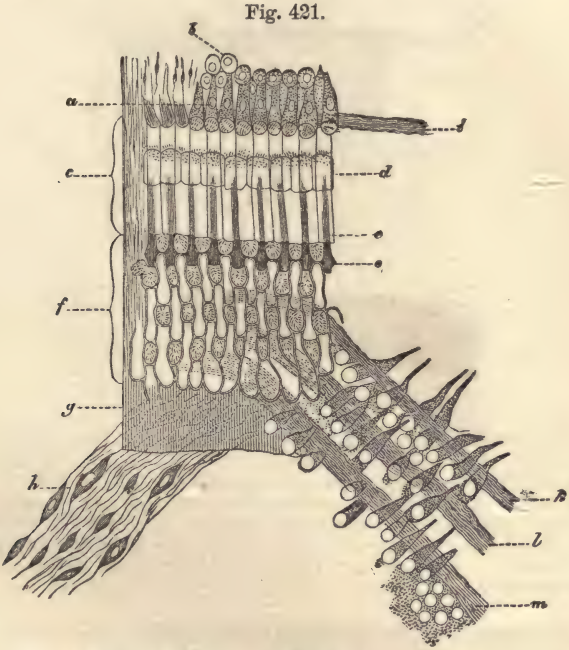

Fig. 421. Organ of Corti, from Man (a Woman, twenty-eight years old). Surface view; teased preparation; spiral bands of fibres. $\frac{400}{1}$. *a*, inner hair-cells; *b*, small round cells of the sulcus spiralis internus; *c*, head-pieces of Corti's pillars; *d*, small punctate formations on the pillars; *e*, head-plate of an outer pillar, shining through the head-plate of the inner pillar, and passing continuously into the first phalanx e_1; *f*, lamina reticularis with four rows of hair-rings and four rows of phalanges, which pass continuously into a row of large plates (Deiters' terminal frames); *g*, membrana basilaris; *i*, inner band of spiral fibres; *k*, *l*, *m*, three outer bands of spiral fibres, with intervening outer hair cells; *h*, connective tissue with spindle-cells from the tympanal surface of the membrana basilaris.

divisions of the outer band, notwithstanding the fact that here there are more rows of hair cells, and, as Löwenberg states, the spiral fibres are more easily seen than in other animals. Very often (see fig. 421) in teased preparations we obtain fragments of the bands of fibres with the hair cells lying between the individual bands, and firmly adherent to them; I have never succeeded, however, in demonstrating a connection between the fibres and the cells.

The fibrillæ of the spiral bands belong to the most delicate structures known in histology. With the weaker magnifying powers they appear—as already stated by Hensen (27), who compares them with the molecular layer of the retina—quite like a finely granular mass, or like a finely

fibrillated neuroglia. With very powerful lenses they display extremely delicate, irregular varicosities, which, however, resemble more closely the granular swellings already mentioned by me when speaking of the very delicate connective-tissue fibrillæ; from the delicate drop-like varicosities of the radial primitive nerve-fibrillæ these swellings can be clearly distinguished.

Fig. 422.

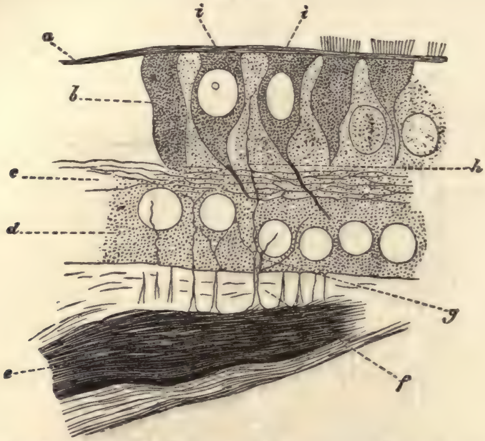

Fig. 422. Longitudinal (spiral) section of the organ of Corti, involving the region of the inner hair cells. Vesperugo noctula. $\frac{800}{1}$. *a*, cuticula (section of the inner portion of the lamina reticularis) with a few prominent tufts of hair; *b*, inner hair cells, two of which have long, somewhat shrunken processes; *c*, spiral fibres; *d*, granular layer; *e*, bundle of nerves (oblique section); *f*, a few nerve-fibres passing through the granular layer; *g*, a nerve-fibre which subdivides in the granular layer into several fibrillæ; *h*, a longer and more delicate nerve-fibre, which passes upwards between the hair-cells.

To this difference between the spiral fibres and the outer radial terminal nerve-fibres—as shown in fresh preparations which have been treated with pérosmic acid—I would call the reader's special attention. In proof of the fact that I actually had the spiral bands of fibres of Corti's organ before me, and that they were not confounded with tympanal fibres, ample evidence will be found in figs. 421 and 422.

I am unable to state positively at the present time what is the origin of the spiral bands of fibres of the organ of Corti, and what their signification. All the information that we can obtain is to be looked for in the region of the inner hair cells, where the nerves emerge and where the above-mentioned granular layer is situated. Appearances similar to those given in fig. 420 may be obtained from teased preparations of this by far the most important part of the organ of Corti. Between the hair-cells and the openings of the foramina nervina lies a stratum of small round cells, with relatively large nuclei and a protoplasm so extremely delicate that we can rarely see it in a state of perfect preservation. From these cells—which for the time I will designate as "granule cells"—are given off in different directions processes which very closely resemble the fibrillæ of the spiral bands, and even (at *d*) seem to bend round and continue their course with them.* In longitudinal

* Unfortunately the drawing of fig. 420 has not been sufficiently successful to give a correct idea of the delicacy of the spiral fibres here under consideration, and of

sections of the lamina spiralis (fig. 422) the elements of the region of the inner hair cells follow each other in five successive layers: nerve fibres (*e*); granular layer (*d*); layer of spiral fibres (*c*); between its fibres, the processes of the inner hair cells (*b*), imprisoned as it were in a network of fibrils; and lastly the ciliated cuticula (*a*). The nerve-fibres are seen entering the granular layer as large (*g*) and small (*f*) bundles of axis fibrillæ; I have also seen, as at *g*, subdivisions occurring in the larger bundles of fibrillæ.

Fig. 423.

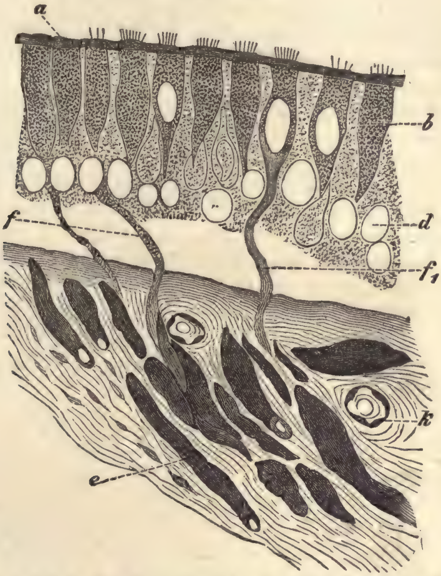

Fig. 423. *a*, *b*, *d*, *e*, as in previous figure; *f*, nerve fibres passing through; f_1, a similar fibre, which, however, becomes fused with a hair cell; *k*, transversely cut blood-vessel.

A few of the narrow nerve fibrillæ pass upwards between the hair cells; from what has already been said on page 1040, these must be considered as outer radial fibres, which simply pass between the inner hair cells and the pillars, but do not terminate there. I have not been able to decide whether still other nerve fibrils are continuous with the processes of the granule cells, and whether through them—or directly, as Max Schultze (50) and Deiters (13) hold—they are connected with spiral fibres (or bend round into them)—which would compel us to consider these last as primitive nerve fibrillæ (Max Schultze).* I shall confine myself in this place, so far as I

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the difference between them and the varicose nerve fibrillæ (also imperfectly drawn in the figure); these last were taken from another preparation and introduced here for the purposes of comparison (*k* and *l* in the figure).

* From a written communication, to which the author has very kindly allowed me to make reference here, it appears that Max Schultze's statements concerning the direct bending round of the non-medullated acusticus-fibres into spiral bands of fibres were based chiefly on a series of preparations from the Human cochlea. Max Schultze compares this layer of spiral non-medullated nerve-fibres with the optic-fibre layer of the retina, into which the medullated optic-fibres bend directly.

am able, to the simple statement of facts; farther on I shall return to the consideration of the *rôle* of the spiral system of fibres.

Cochlea of Birds and Amphibia.

The cochlea of Birds, compared with that of Mammals, displays a simpler structure. In the body of the cochlea we find stretched out between two cartilaginous rods a membrana basilaris; opposite to it the already described tegmentum vasculosum, which serves as a cover for the ductus cochlearis. The internal lining of the ductus consists of epithelial cells of different size and form, of hair cells and granule cells—these last two forms, however, occur only in those places where nerves approach the wall of the cochlea-and of a membrana tectoria.

The large epithelial cells are cylindrical and very clear and transparent; they have the greatest length on the so-called auditory teeth—projections from the under quadrangular cartilaginous rod; Hasse (20) terms them "tooth-cells;" according to his account, they probably play a part in the formation of the membrana tectoria. The latter is spread out over the entire region of the hair cells, but is at no point attached to it; in the lagena it possesses a purely mucous consistency and contains numerous otoliths. On its tympanal surface it displays a regular mosaic of the impressions of the hair cells, whose cilia project into the substance of the membrane. The hair cells themselves occupy, as in Mammals, only a certain zone of the body of the cochlea; the blind extremity, however, of the lagena is completely filled with them.

Fig. 424.

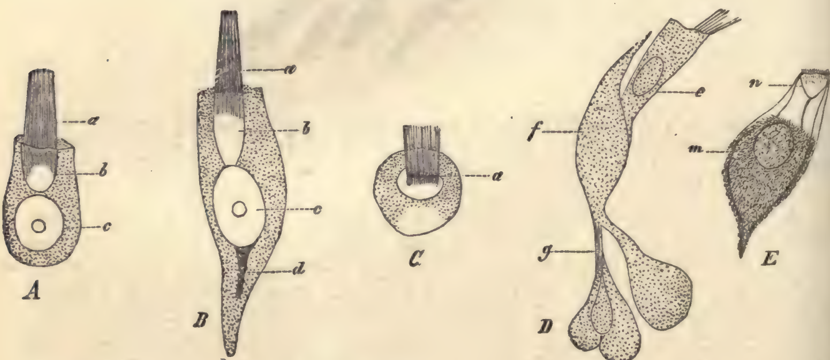

Fig. 424. Isolated cells from the cochlea of the Dove. $\frac{800}{1}$. (Fresh, in a 0.5 p. c. solution of ordinary salt). *A*, *B*, *C*, hair cells; *A* and *B*, a length-view; *C*, an end-view; *a*, tuft of hair; *b*, a clear, chalice-shaped space; *c*, nucleus with nucleolus; *d*, basilar process, with a dark thread reaching to the nucleus; *D*, a group of small, cell-like bodies, which are connected with a tooth-cell (*f*) by means of stem-shaped processes (*g*); *e*, hair cell; *E*, tegmental cell; *m*, darkly granular, nucleated cell-body with transparent terminal portion (*n*).

Each hair cell is surrounded by a circle of cylindrical, clear epithelial cells—Hasse's tooth-cells; it possesses a cylindrical form (its lower part bulging out somewhat) and terminates in a long process. Its upper end carries a large tuft of delicate stiff hairs of considerable length. Deiters

(14) and Hasse (20) describe, as did Leydig (36) at an earlier date, only a single broad, long hair on the end surface of the cells, and, disregarding the fact observed by them that sometimes this apparently solid hair shows signs of breaking up into individual smaller hairs, they still hold fast to this decidedly wrong interpretation of the matter. For this reason they name the structures we are speaking of "rod cells," a name which I believed it would be better to exchange for that of "hair cells," if for no other reason, at least to express the correspondence of these cells with the inner hair cells of Mammals, which they most resemble. In a surface view the tuft of hair appears as if it rose out from a goblet-shaped depression in the cell, and extended, in the opposite direction, almost down to the nucleus. The upper free end of the cell is provided furthermore with a cuticular rim. I have also sometimes seen a delicate thread running from the nucleus to the basilar process of the cell. Hasse draws something similar to this from the Frog, and from the apparatus of the semicircular canals in Birds; there, however, the dark line runs from the nucleus of the cell to the free surface.

Both in Birds and in Frogs Hasse (18–24) has demonstrated the direct passage of the undivided non-medullated nerve fibres into the basilar processes of the hair cells; this was the first trustworthy observation of the termination of nerves in the cochlea. From my own preparations, which were taken from the Dove, I can corroborate his statements; the relations are quite the same here as in the inner hair cells of Mammals (fig. 423). The granule cells are also present in Birds; they form a narrow layer at the base of the hair cells, just above the point of emergence of the nerves, and are also connected with delicate processes. Hasse (21, 22) considers them as stunted epithelial cells.

Among the lower animals my experience is too limited to justify any statements of my own. According to Hasse (23–25) the internal lining of the cochlea and the termination of the nerves in Frogs are the same, in the main, as in Birds; this statement, according to Leydig and Deiters, would also apply to Reptiles—except as regards the termination of the nerves, which was not observed. I will repeat the remark that structures resembling the pillars of Corti—the outer hair cells and the lamina reticularis—do not occur outside of the Mammalian class.

Remarks on the Comparative Anatomy and Physiology of the Cochlea.

The anatomical facts prove beyond a doubt that the inner hair cells constitute the most essential part of the cochleal apparatus. It should be remarked here that the hair cells of Amphibians, Reptiles, and Birds, in structure and position, resemble more closely the inner hair cells of Mammals, in which class the organ of Corti and the outer hair cells come in as entirely new elements, which reach their highest development in Man. In Mammals undivided axis-cylinders serve as the terminal nerve fibres for the inner hair cells, in precisely the same manner as observed by Hasse in Birds and Batrachians. The inner hair cells are never double cells, nor are they attached in the manner that is peculiar to the outer hair cells. Whether or not in Mammals other special structures, corresponding to Hasse's tooth-cells, lie between the inner hair cells—as sometimes appears to be the case in longitudinal sections of the lamina spiralis—I am at present unable to determine. The arch of Corti should unquestionably be considered as an apparatus that is destined chiefly for the support of the hair cells.

The membrana tectoria and the mass of otoliths require further consideration. Hasse (20–24) has placed both of these structures in one category

and interpreted them as vibrating apparatuses, whose vibrations (communicated to them from without) are transmitted directly to the ends of the nerves through the medium of the cilia of the hair cells; he believed, therefore, that of the structures in the internal ear these were the ones whose particular function it was to excite the sensation of hearing—a view which, as is well known, had already for a long time been accepted for the otoliths. I myself would ascribe to these structures a function no less important, but directly the opposite of that held by Hasse: I would consider them as *apparatuses for damping the sound.* Helmholtz (Tonempfindungen, etc.) has shown that, in connection with the apparatuses of the internal ear, a very perfect mechanism for damping must necessarily exist, and I believe that no portion of the labyrinth could be better adapted, by reason of its anatomical construction and position, to perform this function than the membrana tectoria and the otoliths. The latter are usually aggregations of small crystals, suspended without any regular order in a mucous mass, which in turn lies upon the auditory hairs. Even the large, simple otoliths of Fishes and other animals are in reality agglomerations of countless small crystals. The reader will surely agree with me that such an apparatus, which reminds one of a sand-bag, can scarcely be capable of performing regular vibrations, but that it is much better adapted to damp the vibrations of other bodies with which it comes in contact. In favor of this view I would mention the observation made by Hensen * that the Decapods make use to a certain extent of whatever particles of quartz or crystals of uric acid may be thrown in their way, to replace the otoliths which they lose at every change of skin.—The mucous consistency of the membrana tectoria, of which mention has already been made, and its perfectly free position, stretching as it does like a veil of jelly over that portion of the auditory end-apparatus which carries the hair cells, adapt it far better, I think, to serve as a damping apparatus than in the manner ascribed to it by Hasse.

Corti's Organ and the Retina.

It is not foreign to our subject if at this point we inquire into the morphological relation between those two apparatuses of sense whose duty is to transfer regular vibrations to the nerve termini. A comparison seems the more called for since the writings of Stricker, Schenk, Török and others have shown that there is no essential genetical difference between labyrinth vesicle and primary optic vesicle, since at least in the Batrachia both originate from the same germinal layer, the sensorial layer. It is true that our inadequate acquaintance with the development prevents us from instituting a detailed comparison, yet associating what is already known with the matured organs furnishes us with a parallel which I should like to draw here, even if more or less imperfect. That sclera and bony cochlea correspond to one another, none will deny; I refer to the bony formations in the sclera of Birds, and the cartilage in the sclera of Batrachia, etc. The connective tissue wall of the ductus cochlearis is the homologue of the choroid, and the scalæ (comp. page 1017) seem like very strongly developed perichoroidal spaces. The lamina fusca, too, of the sclera is not wanting, for the periosteum of the cochlear wall as well as the more central delicate portion of the outer cushion of connective tissue (figs. 408 and 409) bear the same large-branched pigment bodies as the sclera does. The corpus ciliare is evidently represented by the stria vascularis, which in fact in Birds exhibits, as tegmentum vasculosum, the very same formations as we have already seen in the processus ciliares.

To carry the comparison further we must remember the fact that in the eye a depression of the optic vesicle takes place, so that it takes the shape of a beaker, whose pedestal represents in a certain degree the opticus, and whose walls, as the immediate result of the bowing in, must be double (Kölliker (62) pag. 276). The two lamellæ of the secondary optic vesicle thus formed, whose shape resembles a beaker with the

* *Zeitschrift für wiss. Zool.*, Bd. 13, 1863, p. 319 et seq.

cavity looking forwards, pass continuously into each other along the edge of the beaker; the outer lamella is continued into the optic nerve; the inner constitutes alone the floor of the beaker and develops into the retina; the outer forms the tapetum nigrum. Such a complete depression does not take place in the ductus cochlearis. If, in the case of the primary optic vesicle, we imagine the process of depression to have been arrested soon after its commencement, the optic vesicle will then appear like a bladder flattened on the side where the depression started, and in cross-section it will look somewhat like the sections of the ductus cochlearis represented at e_3 and e_4 of fig. 407. The flattened side in the process of being depressed (the tympanic in the figure) would be that very one which developed itself into the retina; the intermediate space between the layer of rods and the pigment epithelium, which disappears subsequently by the depression being carried to its utmost limits, remains unaffected; we should have here a wall of the primitive optic vesicle (here the tympanic, fig. 407 e_3) whose cells became developed in the intermediate space into the special elements of the retina; while all the rest of the inner surface of the vesicle was invested with the short columnar pigment epithelium of the tapetum nigrum, which, however, passes continuously on all sides into the cells of the retinal pillow, the optic terminal apparatus. Such are the actual relations in the ductus cochlearis. Its intermediate space corresponds with the intermediate space of the primitive optic vesicle; in place of the depression at one point, the innermost layer of its wall (that is, the one originating from the sensorial layer, and corresponding to the primitive optic vesicle) is developed to a nerve pad, the acoustic terminal apparatus (Corti's organ), which instead of having the form of a disk has that of a zone-shaped plate, and whose innermost cell layer (hair-cells) forms a gradual transition into the other epithelial formations of the duct.

In histological details also there is a similarity between the retina and Corti's organ. The epithelium has in the latter, as in the cells of the tapetum nigrum, granular pigment; the only difference being that in the ductus cochlearis it has a lighter color. In Man these pigment granules also, as previously mentioned, lie in the lamina reticularis.

For further details I must refer to the section shown in fig. 422. I find the layer of rods and cones, as also the outer layer of granules, represented in Corti's organ by the hair-cells; the outer segments of the rods correspond to the hairs; the protoplasmic body of the hair-cells is the homologue of the soft inner segments, the rod or cone granules. In the retina, as we observe, a finer subdivision has taken place. Thus the rods might be regarded as the morphological equivalents of the outer hair-cells, the cones of the inner; at least the relations of the nerves point to that direction, since tolerably thick bundles of axis fibrillæ pass to the inner hair-cells exactly as to the cones, while on the other hand the outer hair-cells, like the retinal rods, contain only fine solitary fibrillæ. It may well be surmised that physiological differences exist between the inner and outer hair-cells, as Max Schultze has shown us in the rods and cones. The stout cuticular formation of the lamina reticularis would be without its homologue in the retina if we were not to compare the limitans externa with it, and yet at the same time serious objections might be raised against such a comparison.

The spiral fibre bands of Corti's organ (fig. 422) can certainly be compared with the intermediate layer of granules, and the acoustic layer of granules (d) finds its counterpart in the inner granular layer of the retina; at any rate, the entire microscopic relations of the two strata agree in the principal points. The layer of ganglionic cells, shown in the ganglion spirale, are at a great distance in the ductus cochlearis; consequently there is no strict homology with the molecular layer of the retina; in place of this, however, may be taken the fine retiform connective tissue which surrounds and accompanies the fibres of the acoustic nerve from the ganglion to the entrance of the foramina nervina. In making a thorough comparison there is one thing further to be taken into account, viz.: that the elements of the retina are for the most part disposed in layers which are at right angles to one another, while those of Corti's organ, at least so far as the group of outer hair-cells is concerned, are arranged in layers parallel to one another, similar to what is observed in the retina at the macula lutea.

A formation corresponding to the lens and the vitreous humor must not be looked for in the ductus cochlearis. I am well aware how incomplete the comparison must still remain for the present; still I have been desirous of making this sketch, because we may expect to understand the labyrinth more thoroughly if our studies are prosecuted in this direction, though morphological and physiological identity are often very far apart.

Controversial Points and Historical Notes.

We shall limit ourselves strictly to the main points at issue, in alluding to the statements of other authors whose views differ from those advanced here. It is impossible in this present work to enter minutely into the details of each cochlear structure, which is interpreted about as variously as in the retina.

First of all we shall observe that Deiters (13), Löwenberg (37–39), and Henle (26) maintain that the *membrana tectoria* is attached to the outer wall of the ductus cochlearis in the vicinity of the ligamentum spirale accessorium. Gottstein and I have never seen this attachment in the large number of our sections through the cochlea, most of which were successful, nor have we seen it in other sections prepared by injection with gelatine, nor have Kölliker (30), Middendorp (40), and Rosenberg (49) had any better success. Further, the plates of Löwenberg and Henle, too, do not correspond. Accordingly Löwenberg's fourth cochlear canal (canal que j'ai découvert, Löwenberg), Henle's upper chamber, must be given up. Deiters (13) and Henle (26) furnish the most detailed description of the *crista spiralis.* The former regards the small epithelial cells found there as connective tissue. Hensen (27), with whom Kölliker (30) and Middendorp (40) are inclined to agree, believes the basis substance of the crista, which I hold for osteoid substance, to be an epithelial secretion. Henle was the first to prove the connection between the warts of the crista and the teeth; he also demonstrated thickenings, tubercular in form, on the tympanic surface of the membrana basilaris. From the two forms of the *lamina reticularis* which Henle describes I can only recognize the second as the normal one; the former is an artificial product of the latter. This lamina is best seen in fresh preparations.

Henle (26) has also described two different forms of inner *pillars*, as to the truth of which I must range myself with Middendorp (40), and doubt it. This latter author as well as Deiters (13) believes them to be hollow; actual cross-sections, which I have often enough seen both in my own and in Gottstein's preparations, show them to be quite solid formations resembling close bundles of fibres. In opposition to the lately revived statement of Kölliker (30), that the outer pillars have varicosities, I can only assert that I have never been able to see them, under any circumstances; this matter, however, is of no importance at present.

Löwenberg (39) describes processes at the lower end of the inner *hair-cells* which branch and unite with the processes of the granule-cells, a condition of things which I have never yet seen.

The most minute description of the outer *hair-cells* is furnished by Deiters (13). All later observers of the cochlea in Mammals are for the present obscured by the brilliancy of this excellent investigator. Gottstein's explanation of the outer *hair-cells*, which is accepted in the present article, deviates in the following respect from that of Deiters. The latter claims for the outer slope of Corti's organ two entirely separate forms of cells which are only united with one another by their processes. The one bearing hairs (rod-cells, Deiters) passes directly into the basilar process (connecting pedicle, Deiters), and is firmly attached to the rings of the lamina reticularis. Between the rod-cells quite *independent* spindle-shaped cells appeared [hair-cells, Deiters, Deiters' cells, Kölliker (30)], whose upper process passes over into a phalanx, the under one into the attachment-pedicle of a rod-cell. I am unable to distinguish, as Gottstein does, the spindle-shaped cells of Deiters as entirely separate formations from the hair-cells; at any rate the semi-diagrammatic plates in the manuals of Kölliker and Frey (figs. 512 and 571) are in no way suited to furnish a true representation of the real relations of the parts. I have always found that every two conical cells were united into a double body. The so-called Deiters' cells of the authors can be compared morphologically with Hasse's tooth-cells of Birds (compare loc. cit. (24), tab. 27, fig. 8), yet are here consolidated in a curious way with the hair-cells.

The greatest differences still prevail in the statements about the relations of *cochlear nerves;* there is hardly a possible kind of nerve termination that has not been found by some author. Disregarding terminal loops (R. Wagner, Harless (17)), and the passage of all or at least some nerve bundles upon the tympanic surface of the membrana basilaris (Corti (10), Böttcher (2) Max Schultze (50), Deiters (13)), which views can certainly be no longer maintained by their originators, all observers admit, since the discoveries of Kölliker (33), and Max Schultze (50), that the nerve fibres enter the ductus cochlearis through holes in the membrana basilaris, and there either extend onward exclusively in a radial direction (Rosenberg (49), Böttcher (4), Middendorp (40)), or in a radial and spiral manner (Max Schultze (50), Kölliker (30), Deiters (13), Hensen (27), Löwenberg (39)). All observers, too, are united as to the

existence of the radial nerve fibres. Still we find but few positive statements as to their termination attested by figures, and such only can be noticed here, for it is impossible to allude to all the suppositions which have been expressed without the support of some proof. We shall mention those of Böttcher, Rosenberg, Middendorp, and latest those of von Winiwarter (57). These, apart from the interesting discovery of Hasse in the cochlea of the Bird and Frog (*vide* page 1047), are the only positive expressions in regard to the radial nerve termini in the cochlea. Böttcher repeats his views, laid down repeatedly in 1859, that the nerves, after their passage through the habenula perforata, pass over in part into the cells lying on the inner row of rods, in part, too, under the arch, and here run transversely through to Corti's rows of cells. As to whether any precise mode of termination is claimed here is unfortunately not to be deduced from the verbally quoted references, which were the only ones at my disposal; to obtain further details we shall have to wait for the complete work promised by Böttcher.

E. Rosenberg mentions only the termination at the outer hair-cells, but his statements are on the whole correct, and he is certainly the first who has given a drawing of this condition. It is true that he forgets at the same time to say that this figure is in good part diagrammatic; I can at least not repress some doubts of the existence of one of his preparations which corresponded to fig. 3, Plate II. Whoever is moderately acquainted with the hair-cells, the cells in the sulcus spiralis internus, and Corti's arches, will assent to this without further comment.

Middendorp, on the other hand, is only acquainted with the inner radial fibres, which he believes unite with the cells of the acoustic granule-layer and then terminate freely between the inner hair-cells. Von Winiwarter, as well as Rosenberg and Gottstein * observed the termination of the outer radial fibres in the outer hair-cells; in regard to the relation of nerves to the inner hair-cells no views are advanced in his present work.

Max Schultze (50) is the discoverer of the spiral fibre-bands in the cochlea; the existence of these structures has been confirmed lately by Deiters (13), Kölliker (30), Hensen (27), and Löwenberg (39); the latter has furnished the most complete description of them. The above-mentioned authors agree with Max Schultze (*vide* page 1045) as to their nervous character. Besides the discoverer no one, however, advances positive views in regard to the mode of termination of these fibres in the cochlea. According to the views represented in the present work the spiral nerve-fibres become connected with protoplasmic remains at the feet of the inner pillars, and also with cells which lie at the apex of the arches, probably also with the external hair-cells.

In addition to the bands whose existence I have confirmed, Deiters (13), Löwenberg (39), and Kölliker (30), describe spiral fibres on the inner side of Corti's arch. According to Max Schultze (50) there are also spiral fibres within the arch itself.

It is unquestionable that these spiral bundles of fibres are still the most obscure part in the anatomy of the cochlea. My opinion is that they should be considered as connected with that small layer of coarsely granular delicate cells in the sulcus spiralis internus which I have compared with the inner granule-layer of the retina, and for which I recommend the name of acoustic granule layer (*vide* fig. 422). For this layer, as also for the spiral fibres, the same different interpretations are admissible, which I at this time insist on for the inner granule-layer of the retina, or the granule-layer of the cerebellar cortex. (Comp. my work in the *Zeitschrift für rat. Medicin*, 1863, Band XX.) So have also, in fact, Max Schultze (50), Deiters (13) in part, and Middendorp (40) connected them with the nerve fibrillæ as small bipolar ganglionic cells; while Deiters (13), on the other hand, denied any nervous character for most of them, and Rosenberg (49) and Hasse (21) for all formations. Rosenberg's (49) statement is worthy of note, viz., that their number is greater in young animals—a fact which Gottstein was able to confirm in young Dogs. Hasse (20) made the same observation in Birds; the latter (24), page 409, denies all relations of the formations lying between the hair-cells and below them to nerve fibres.

In stating my views in regard to the cells and fibres which are the subject of dispute I will say that the observations which I have made with positiveness in regard to the nerve-endings make it probable that neither the granule-cells nor the spiral fibres have a nervous character; otherwise we should be obliged to claim a double nerve ending. The difference between the well-established radial nerve fibres and the spiral fibre-bands (see page 1041) opposes this supposition. Accordingly all that remains for us is to conclude that these fibres and cells are to be regarded as a delicate neuroglia, and to compare it with the non-nervous elements of the inner granule-layer

* *Centralblatt für die medicin. Wissenschaften*, No. 40, 1870.

and intermediate granule-layer of the retina. Still this point can only be determined by further careful examinations based on embryological researches.

The older literature of the cochlea is recapitulated pretty thoroughly by Hildebrandt-Weber (Aufl. 4, Bd. iv. page 7); in addition one may compare the writings of Deiters (13). The histology of the cochlea, excluding certain discoveries of Huschke's (28), dates from the investigations of Corti (10) (pillars, outer hair-cells, ganglion spirale, stria vascularis, Corti's membrane, etc.). Reissner (46) furnished very valuable contributions, which first made it possible to gain an accurate morphological conception of the cochlea (Membrana Reissneri ductus cochlearis); Hensen (27) gave us the canalis reuniens, blind commencement and end of the ductus cochlearis, collection of cells in sulcus spiralis int., and many single points, and Kölliker contributed embryological investigations, development of Corti's organ from epithelial cells, lamina vascularis, which he discovered contemporaneously with Max Schultze (50), secondary formation of the scalæ, passage of nerves through the foramina of the habenula perforata. Further, we have received important contributions from Max Schultze (spinal fibres, layer of granule-cells, basilar processes of the outer hair-cells, continuation of the fibres of the auditory nerve as non-medullated primitive fibrillæ quite into the organ of Corti, etc.) and from Deiters [(12–15) inner hair-cells, first accurate description of the outer hair-cells, and of the lamina reticularis, as also a number of details on almost all parts of the cochlea, the accuracy of which every good preparation testifies to]. Deiters' description has been decidedly the standard of all later researches on the cochlea. Other valuable details are due to Reichert (blind sac of the vestibule, excellent morphological description of the cochlea, and especially of the ductus cochlearis) and to Böttcher [(1–4) inequality in number between the inner and outer pillars, which he also described very minutely; their arcade-like course; both simultaneously published by him and Claudius]. The granule cells in the sulcus spiralis, also the inner hair-cells, Böttcher appears to have been the first to see, though he gives no very exact definition of them. Claudius furnished the first histological facts in regard to the cochlea of Birds. For the more recent contributions of Henle (26), Middendorp (40), Löwenberg (39), Kölliker (30), and Rosenberg I must ask the reader to consult the list.

Apart from what Leydig (36) furnished at different times, containing, it is said, the first notice in regard to the appearance of hair-cells, the comparative histology of the cochlea rests principally, and thus far almost entirely, on the thorough works of Deiters (14–15) and Hasse (18–25), which also essentially enlarge the older descriptions of Windischmann and others. Here, also, mention must be made of the comparative anatomical researches of Hyrtl (29) and Claudius (7–9), which offer much that is interesting.

For the embryological history of the cochlea I allude to the works classified between Nos. 58 and 65 of the bibliographical list, to which must be added the articles by Huschke (28), Reissner (46–47), Kölliker (34), Hensen (27), Hasse (20), Böttcher (4), Rosenberg (49), and Middendorp (40).

Some portion is found in the text; a connected statement of the cochlear development would scarcely be possible at the present time.

Methods Employed in the Investigation.

I do not think it necessary to recommend that the cochlea be examined in the fresh state, and in aqueous humor. Quite as good views, and indeed more serviceable, on account of the somewhat sharper contours, are furnished by perosmic-acid preparations, and I should maintain that they were just as important for the cochlea as for the retina. A strength of from $\frac{1}{10}$ to 1 per cent. may be employed. The former is to be preferred for preparations that are to be teased apart; the latter for hardened preparations. A $\frac{1}{4}$ to $\frac{1}{2}$ per cent. solution of common salt is also very serviceable for fresh preparations that are to be torn apart. The pillars are most easily isolated in a 5-per-cent. solution of chromic acid; a solution of chloride of gold is recommended by Cohnheim for the cornea, and a 1 per-cent. solution of nitrate of silver as well. The latter is advantageously employed for the spiral fibres. For obtaining good sections I should recommend the adoption of the following plan: Take a large cochlea; remove as much of the bony substance as possible by means of very powerful cutting pliers, then open the cochleal house in three or four places; little cochleæ, however, should remain intact. They should then remain twenty-four hours in a pretty large quantity of chloride of palladium, 0.001 per cent., or in a perosmic-acid solution from 0.2 (for smaller cochleæ) to 0.5–1 per cent. (for larger ones). Then the preparation should be treated twenty-four hours with absolute alcohol, should be brought immediately into the fluid that deprives it of its earthy

salts. The best fluid for this purpose is chloride of palladium (0.001 per cent.) with $\frac{1}{10}$ part muriatic or chromic acid ($\frac{1}{4}$ to 1 per cent.). After this process is completed the cochleæ should be washed in absolute alcohol, and enclosed in a fresh piece of marrow or liver. In large cochleæ it is easy to cut out a suitable piece from the latter. Then the preparations, together with the enclosing substance, should be replaced in absolute alcohol. In hardening, the latter contracts so firmly about the cochlea that it lies immovable in it, and can conveniently be divided into the smallest pieces. The hollow passages of the cochlea can be filled with gelatine and glycerine (equal parts), or a mixture of oil and wax, before they are enclosed. (*Vide* page 1 of this Manual, "Stricker's General Method," and Klebs, in the Archiv für Mikroscop. Anatomie, vol. v. 1869, page 164). I prefer the gelatine and glycerine mixture unquestionably; and I regard filling the cavities according to the plan given above as superfluous, and only possibly of advantage in maintaining the position of Corti's membrane. My best preparations, from which the drawings have been taken, were not from cochleæ filled in this way. It is important to use a sharp knife.

TABLE OF MEASUREMENTS.

The following table contains an enumeration of the most important measurements in Man. I have intentionally made use of round numbers in every case, because there is no object to be attained beyond preserving approximate data. For comparison, some measurements from the Dog and Vesperugo are added. In estimating the number of the pillars and hair-cells the length of the lamina spiralis is calculated at 30 millim.

NAME OF PART MEASURED.	OBSERVER.	MAN.	DOG.	VESPERUGO.	REMARKS.
1. Canalis reuniens, length of.....	Hensen.	700			
" " diameter......	"	220			Narrowest part.
" " thickness of the wall..		15			
2. Lamina spiralis membranacea. Total length in two full-grown men..........................	Waldeyer.	28 to 31 mm.			In the vicinity of Corti's organ.
3. Ductus cochlearis. Breadth from the beginning of the crista spiralis to the lig. spirale—					
1st turn..................	"	800	700	360–400	
2d turn..................	"	700	"	350	
4. Ductus cochlearis. Greatest height—					
1st turn..................	"	500	400–450	400	
2d turn..................	"	"	350	260	
5. Length of Reissner's membrane—					
1st turn..................	"	900			
2d turn..................	"	700			
6. Crista spiralis, breadth of the—					
1st turn..................	"	300	150	140–150	
2d turn..................	"	200–250			
7. Auditory teeth, length of the....	Henle.	30			
Breadth of the..............	"	12			
8. Sulcus spiralis internus. Greatest height..................	Waldeyer.	60–70	60–70	100–120	
9. Space between the basal points of insertion of Corti's pillars..	"	66–70	80–90	40	Measured in hardened preparation. 1st–2d turns.
10. Height of the semi-circular canal. (Size of calibre)........	"	12	40	21–24	
11. Length of the inner pillars measured on the dorsal side from the basal points of insertion to the ridge of the arch..........................	"	50	60–70	45	In hardened cross-sections. The appended plate is not included in the measurement.
12. Length of the outer pillars taken in the same way.........	"	60–66	90	50	
13. Thickness of the body of the pillars—					
Inner..................	"	4.5	"	"	
Outer..................	"	3.	"	"	
14. Cell bodies of the inner hair-cells					From a new-born child. The length is somewhat approximative, since observers are not decided as to where these processes begin.
Length..................	"	18	"	"	
Breadth..................	"	6–9	"	"	
15. Outer hair-cells. Total length with basilar process...........	"	48	"	45	Half of the length comes out of the process.
Breadth..................	"	6–7	"	6–7.5	

NAME OF PART MEASURED.	OBSERVER.	MAN.	DOG.	VESPERUGO.	REMARKS.
16. Length of the hairs........	Waldeyer.	4	"	"	
17. Phalanges. Average length....	"	15	"	"	
18. Rings. Average diameter......	"	6	"	"	
19. Epithelium of Reissner's membrane— Thickness................	"	9	"	"	
20. Thickness of epithelium in sulcus spiralis ext..............	"	15	"	"	
21. Greatest radial breadth of the membrana sectoria...........	"	200–230	"	"	
Greatest thickness.............	"	50	"	"	
22. Nuclei of the granule cells......	"	3.5–4.5	"	"	
23. Ganglionic cells from the ganglion spirale.................	Kölliker.	24–35	"	"	In the first turn there are 40 to a millim., at the Hamulus there are about 80.
24. Number of foramina nervina...	Waldeyer.	3,000	"	"	
25. Number of the inner pillars.....	"	6,000	"	"	
26. Number of the outer pillars.....	"	4,500	"	"	
27. Number of the inner hair-cells..	"	3,300	"	"	4,500 in every row, the rows being equal in numbers to the outer pillars.
28. Number of the outer hair-cells..	"	18,000	"	"	

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61. REMAK, Untersuchungen über die Entwickelung der Wirbelthiere. Berlin, 1855. Fol.
62. KÖLLIKER, Entwickelungsgeschichte des Menschen und der höheren Thiere. Leipzig, 1861. 8.
63. SCHENK, MOLESCHOTT'S Untersuchungen zur Naturlehre. Bd. 9.
64. STRICKER, Zeitschrift für wissenschaftl. Zoologie. Bd. 10.
65. TÖRÖK, MOLESCHOTT'S Untersuchungen zur Naturlehre. Bd. 10.
66. GOTTSTEIN, J., Beiträge zum feineren Bau der Gehörschnecke. Centralblatt für die medicinischen Wissenschaften. 1870. No. 40, 10. September. (Vorläuf. Mittheilung.)
67. BÖTTCHER, A., Einige Bemerkungen zu den neuesten Entdeckungen in der Gehörschnecke. (Fliegendes Blatt, Dorpat, 6. November, 1870.—BÖTTCHER states that most of the facts recently published by Gottstein (66) had already been mentioned by him in his treatise (see No. 3 of this list), which was handed in to the Leopold Academy in September, 1868, but has not yet been published.—The author regrets that he was not able to make use of this treatise of Böttcher's in the foregoing essay, particularly as it referred in a special manner to the development of the cochlea—at least so I infer from a report that Böttcher has had the kindness to send me ("Mélanges biologiques tirés du Bulletin de l'Acad. impér. des Sc. de St. Pétersbourg, T. VII, 23. April 1870,"), in which is printed a short notice by Kölliker of Böttcher's manuscript.

CHAPTER XXXVIII.

DEVELOPMENT OF THE SIMPLE TISSUES.

By S. STRICKER.

The status nascens of a Mammal begins with the fructification of the maternal germ. The fructified germ is a single-celled organism, which afterwards by subdivision becomes many-celled. When the subdivision or segmentation has gone on to a certain limit, the young cells arrange themselves in strata or layers; from the different layers different tissues are developed, and by the combination of certain tissues the different organs are produced. Simultaneously with the arrangement into layers begins the differentiation of the tissues; hence it will be understood why the doctrine of embryonic layers is so peculiarly an object of attraction to histologists.

By the term "embryonic layers" embryologists understand also the membranes with which the embryo later becomes enveloped. These membranes, however, are not in any way intimately related to the histiogenesis; they are only transitory organs, which, like all the other organs, are developed from the primary layers. The doctrine of embryonic membranes is therefore a part of the history of development of organs; and the former cannot be treated of without at least giving an outline-sketch of the latter.

After this preliminary explanation there will be no need of a further introduction. The embryonic layers of cells will occupy our attention only in so far as they may be found to assist us in understanding the histiogenesis.

Mention has already been made of the unimpregnated germ (on page 517 and fol.). To that thorough treatise I have only one or two remarks to add in relation to the nomenclature. I shall always avoid the expressions "plastic yolk" (Reichert),* and "principal yolk" (His). Both expressions, as will be shown later, are based upon erroneous views. Furthermore, the advantage of brevity cannot be ascribed to them, so that no valid reason exists why they should be used in preference to the expression "germ," adopted by Remak. For the same reason it will also be better to call the membrane (Von Baer's Zona pellucida) surrounding the germ germ-membrane, instead of vitelline membrane. It will only be in those cases where the germ has with it under the same membrane a yolk (food-yolk (Reichert), subordinate yolk (His)—as in the eggs of Birds, Scaly Amphibia and Osseous Fishes)—that I shall make use of the terms vitelline membrane or vitelline envelope to designate this membrane.

According to universal acceptation the fructified germ is at first non-nucleated.† One can best convince himself of this fact in the Batrachia, by se-

* The term "Bildungsdotter," in the article referred to, is translated rather loosely by *germ-yolk*, instead of the more exact expression, *plastic yolk*.—TRANSLATOR'S NOTE.

† Johannes Müller (Monatsberichte der Berliner Akademie, 1851, September) is the only authority who has made definite statements concerning the conservation (in Entoconcha mirabilis) of the germinal vesicle and its gradual transformation into the nuclei of the segmentation cells.

curing a pair clasped together during spawning, and then examining separately the eggs already born and those that are still within the body of the mother. It is necessary to select fresh eggs, which should be teased apart with needles; the contents thus set free should be submitted to an examination with very low powers of the microscope, or they should be hardened and sections made from them. In this way it will be ascertained that each one of the eggs taken from the mother possesses a vesicle-like nucleus (germinal vesicle), whose investing membrane can, in a fresh state, be torn apart with needles under a magnifying lens; whereas, in the youngest fructified eggs, no nucleus can be demonstrated. This condition of things is interesting, as it teaches us that a Mammal begins life as a small non-nucleated mass. If we harden these non-nucleated Batrachian germs, we can sometimes, in sections, make out a small cavity, corresponding in size to the former nucleus. This, according to Remak's terminology, is Von Baer's nucleus-cavity. By this designation is implied that, after the disappearance of the nucleus, the cavity in which it lay still persists.

The doctrine is, that if the fructified germ be placed under favorable conditions, there will forthwith be produced within its body a new nucleus. As to this nucleus I can state nothing from actual experience, and it would hardly be profitable to enumerate the different views pertaining to the subject. At this stage the eggs are generally non-transparent, so that in a fresh condition the nucleus cannot be seen. If therefore, notwithstanding this, the formation of a nucleus is spoken of with such positiveness, we must attribute it to the fact that, in the later products of the subdivision of the germ, nuclei may be distinctly made out, which appear to be homogeneous and offer a certain resemblance to oil globules. Taking into consideration the circumstance that the old nucleus vanishes from our view, it is highly probable that we have to deal here with a real new formation.

Before undergoing the process of subdivision the germ passes through a series of individual changes in form.

Mention has already been made on page 523 of the amœboid motions in the germ of the Trout. If we observe atttentively the freshly-laid eggs of Bufo cinereus we shall observe that they possess several facets, and only assume the spherical form later and in a gradual manner. Changes in form have been supposed to take place in the Bird's egg, previous to segmentation, merely from a comparison of the sections obtained from hardened specimens of germs at different stages of development. In this connection we should also mention the observation, first made by Bischoff in the Rabbit's egg, that the yolk (germ) before subdividing receded from the Zona pellucida.

It remains doubtful whether the observation—reported by the same authority—relating to rotations of the undivided germ within the vitelline membrane should also be mentioned in this connection. Bischoff made the observation only in one animal, and since that time nothing has been added to our knowledge concerning rotations * in the unsegmented egg.

Segmentation and the Formation of Layers.

A. Batrachia. The segmentation of the Batrachian eggs was discovered in the year 1824, by Prevost and Dumas,† but it was only in 1826 that its full significance was recognized by Mauro Rusconi. ‡

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* *Entwickelungsgeschichte des Kaninchens*, 1842. On pages 58 and 59 of this work the literature is given relating to the rotations of the yolk.

† *Annales des Sciences*, Sér. 1, Tom. II.

‡ *Développement de la grenouille*, c.

For the study of this process there could not indeed be found a more favorable subject than the Batrachian eggs. With the approach of the first days of spring these eggs may be obtained in large quantities, and if the different species are desired they may be repeatedly found at intervals varying from a few days to several weeks.

It must be borne in mind, too, that the segmentation takes place before our eyes without any interference whatever on our part. It is only necessary to place a string of spawn (Bufo) or a cluster of them (Rana) under water in a shallow dish in order to be able to follow out readily the entire process with the aid of a magnifying-glass. With this mode of observation the germ-membrane remains (by reflected light) invisible, thereby conveying the impression that the germs are about to become furrowed on their surface.

If, however, we place a group of eggs in a small glass dish and examine them by aid of transmitted light, with somewhat stronger magnifying powers (40–50 linear), we shall soon convince ourselves that the transparent membrane takes no part in the segmentation.

The formation of the first furrows in the Batrachian germ can be represented best by drawing a cord around a spherical ball of modellers' clay in the following manner:—First pass a cord over a meridian of the sphere, and then a second cord over a great circle at right angles to the first. In the next place tighten both cords at the upper pole in such a manner that the upper third only of the sphere will be cut through by them. Finally, pass a third cord around the sphere parallel to the equator, at about the boundary between the upper and second third of the axis of the sphere, and then tighten this cord so as to cut the sphere through and through. By this procedure there will be cut off four segments of a sphere, surrounding the upper pole, whereas the larger lower portion of the sphere remains undivided except on its surface, where the two meridian cords indicate the subsequent subdivisions.

The formation of these three furrows takes place gradually. In a temperature of 18–20° C. the process would occupy three or four hours from the act of birth.

Before the definitive establishment of a furrow the surface becomes alternately wrinkled and smooth, repeating the change several times. From the main furrow, moreover, proceed numerous small side furrows, which are only transient in character. Reichert described these side furrows as the circle of folds, and Max Schultze * has shown that they are the expression of motion in the germ.

A cavity is formed at the point of intersection of the three first furrows (which is situated in the upper half of the egg, if it be floating in water). I am unable to say from actual experience whether this cavity coincides or not with the nucleus-cavity. It increases in size by the retraction and rounding off of the confronting angles of the segments.

The next step in the process of segmentation is restricted chiefly to these four upper segments. They subdivide into smaller and smaller pieces, and at the same time the hollow place grows larger, until finally there is produced a spacious cavity (*F*, fig. 425) in the upper third of the egg. With a view to the subsequent steps of the process, we can perhaps best obtain a clear idea of this cavity by imagining to ourselves a spherical apple, whose upper third is so hollowed out that nothing but the skin remains. While,

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* De ovorum ranar. segment. 1863.

therefore, the larger lower portion of the apple is solid, its upper portion is simply a cavity covered only by the thin skin.

We designate the cavity in the Frog's egg by the term "Baer's cavity of segmentation;" the thin dome or shell which covers it, and which is composed of small elements of segmentation, or embryonic cells, we call the "cover" (*D*), and the solid lower half the "bottom" of the cavity of segmentation.

During the growth of this cavity the process of segmentation is also going on steadily in the lower solid portion, but here again it manifests itself more on the surface than in the interior. In this way it happens that very soon the entire egg becomes enveloped in a mantle of small segmentation-sections or embryonic cells. The condition of things now corresponds more fully to the apple partially hollowed out.

The skin of the apple represents the mantle of small cells, while the flesh in the lower solid portion answers to that remnant of the germ which subdivides only very slowly, and still consists, at the time when the mantle has already completed its subdivision, of very large segmentation-sections. But the picture is rendered complete only after we have cut out from the skin, at the lower pole of the spherical apple, a circular piece, exposing the flesh to view in this spot. The progressive diminution in size (subdivision) of the superficial cells does not extend as far as to the lower pole. The small spot (*P*) which is left here is at first irregular then afterwards circular in its outlines, and is composed of large polygonal areas; the centre of the spot coincides with the lower pole.

Fig. 425.

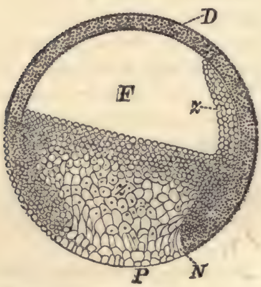

Fig. 425 represents a meridional section of an egg (from Bufo cinereus) whose degree of development does not quite correspond with that described on this page. *F*, cavity of segmentation; *D*, its cover; *P*, white spot at the lower pole; *Z*, germ-cells at the bottom of the cavity of segmentation· *z*, germ-cells which extend up from the bottom of the cavity on to the cover; *N*, section of Rusconi's furrow; *R*, dorsal half; *B*, ventral half.

While in all Batrachian eggs, at this stage, the external surface of the mantle is dark brown in color, this spot remains of a whitish hue—provided the lower half of the egg was of this color originally (Bufo fuseus)—or becomes white, where the lower half of the egg was brown (Rana temporaria, Bufo ciner. and viridis) when freshly laid.

The large white cells, which form the bottom of the cavity of segmentation, and which at the lower pole are exposed to view (*Z*,* fig. 425), were termed by Reichert the "central vitelline mass." Remak held with Rusconi that in the Batrachian eggs there was no element analogous to the vitellus, and therefore substituted the word "gland-germ" for that term. But this term, too, I am unwilling to accept, because the grounds which led Remak to adopt it have been shown to be untenable. These cells are not the only elements that contribute to the formation of glands; they have not even become laminated elements of segmentation, from which the different tissues are developed. For this reason I shall call them germ-cells, thereby intending to convey the idea that their histogenetical character is not yet determined.

* The small *z* in the midst of the germ-cells is evidently intended for a capital *Z*. —Translator's Note.

The germ-cells, at the spot where they are exposed to view, are at first sharply separated by a semilunar fissure (N) from the external mantle, which is composed of smaller cells, and is of a brownish color on the outside. This fissure is called, in honor of its discoverer, the Rusconian * furrow. Later this furrow becomes circular in shape, and the large germ cells, surrounded now by a circular limit, have been designated by Ecker † as the "vitelline plug." That half of the egg in which the semilunar furrow originates I have designated ‡ as the dorsal half, because from it is developed the back of the embryo; the long axis of the back coincides with a line drawn from the middle of the furrow to the upper pole. The opposite half I have termed the ventral half. It was known already to Von Baer that at a later stage the ovules perform in the water a revolution of 90°, thereby converting the meridian into an equator. By this revolution the dorsal half, which was situated laterally, is made to lie on top. This revolution is brought about by the formation of a second cavity, which is stretched out within the dorsal half. By the formation of this cavity, furthermore, the centre of gravity of the ovule becomes displaced, and the revolution follows as a necessary consequence of this displacement. This second cavity (N, fig. 427) was known to Rusconi.§ Golubew, ‖ by historical research, has discovered several errors in the nomenclature of the two cavities; he has also settled the fact that Von Baer's cavity should be called the elliptical, and Rusconi's the semilunar.

Remak ¶ has adopted the view that the Rusconian cavity originates from the furrow of the same name by an extension of the latter into the substance of the ovule, in the form of a diverticle. Theoretical considerations have led him to this belief. He assumed that the Bird's germ was composed of three layers or laminæ of cells. The top or outermost lamina he called the "horny layer," or "sensorial layer;" the second, "middle layer," or "motorial layer," also "motorial and germinative layer;" and finally the third, "intestinal and glandular layer." The fact that the Bird's germ is arranged in layers and bends inwards underneath has been known since the investigations of C. F. Wolf. Now Remak thought that the analogy between the Birds' germ and that of the Batrachia was rendered plausible on the following grounds.

In the cover of the cavity of segmentation he sought for the analogues of the sensorial and motorial layers, while the analogue of the glandular layer in Birds appeared to him to be the little white field at the lower pole of the Batrachian egg. The Frog's germ, he said, is not laminated in its structure, and consequently cannot bend in underneath as in the Bird's germ. Nevertheless the under surface of the spherical Batrachian germ sinks in until it comes in contact with the motorial layer, which, as already mentioned, he imagined to himself as terminating at the inner surface of the mantle-like layer. I have shown,** however, that the Rusconian furrow originates by a separation, and not by a sinking in, of the elementary forms. I noticed, in sections, that from this furrow a delicate trace of separation ran upwards along the dorsal half, in a direction not quite parallel to the surface of the mantle. I therefore believed myself justified in considering this trace of separation as the commencement of the Rusconian cavity, and in assuming that it originated not by a sinking in but by a separation of the elementary forms.

* *Développement*, etc.
† *Icones physiolog.*
‡ *Zeitschrift f.w. Zoologie.* Bd. XI.
§ Müller's *Archiv*, 1836.
‖ Rollett, *Untersuchungen.* Leipzig, 1870.
¶ Loc. cit.
** Loc. cit.

As regards the question of sinking in or separation of the elementary forms, Golubew—the only author who, since the time of my writing, has expressed a decided opinion on the subject—adopts my view of the case. Golubew, * however, speaks of my description of the first steps in the development of the Rusconian cavity as being not exactly in accordance with the facts. I cannot enter, especially in this place, into a discussion of this question; for, in justice to my subject, I can only dwell upon the anatomical details in so far as they are necessary to a clear understanding of the layers. As far, however, as the relations of the fissure to the embryonic layers are concerned, no difference of opinion exists.

Remak has noticed that from the bottom of the cavity of segmentation, at the point where it passes into the cover of the cavity, a group of white germ-cells extend up quite a distance over the inside of the cover (*z*, fig. 425). I have shown, † furthermore, that these outlying cells are of fundamental importance in the formation of the laminæ.

I have shown that the cover of the cavity of segmentation (*D*, fig. 425) serves only as a foundation for the sensorial layer ‡ (Remak), and that from the cells which are deposited on the inner side of the cover are developed the analogues of what Remak has called the middle and glandular layers.

After I had learned that these germ-cells at first extend up on the dorsal half only to an inconsiderable height, but afterwards push their way farther and farther until they even pass beyond the upper pole and approach the germ-cells of the ventral half, which in like manner are pushing their way upwards along the inner side of the cover; after I had learned,§ furthermore, that on the glass slide the cells of the Batrachian germ possess the independent power of changing their form and locality, I expressed the view that the germ-cells, mentioned above, work their way upwards spontaneously, in direct opposition to the law of gravity. This view, too, Golubew ‖ has not been able to share; he believed that the growth of these cells in an upward direction was due to processes of subdivision.

I cannot in this place enter into a discussion concerning our conflicting views. The question as to whether the cells shift their location by wandering or by mutual pressure during the activity of the process of subdivision is in itself a matter of interest, but in its bearings upon the doctrine of the layers it has a subordinate significance. The only point of importance here is the circumstance that the cells actually do become displaced in order to assist in the formation of the embryonic layers—a matter which may now again be considered as settled.

It has already been stated on a previous page that the fissure, which commences at the Rusconian furrow, pursues its course upwards along the dorsal half.

When the semilunar fissure, in the progress of its growth upwards, reaches the limit of the cavity of segmentation, it encounters the aforementioned white germ-cells, which extend up from the bottom of the cavity of segmentation over the dorsal half of the cover. It is into this outlying mass of cells now that the fissure penetrates.

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* Loc. cit. Taf. D, fig. 2.

† Loc. cit.

‡ The same interpretation was afterwards given by Götte. (See Max Schultze's *Archiv*, Bd. 4.)

§ "Ueber die selbständigen Bewegungen, etc.," *Wiener Sitzungsbericht*, 1863.

‖ Loc. cit.

By making a number of horizontal sections through the egg, commencing at the lower pole, it will be seen that the fissure in the dorsal half is nearly semilunar in shape; it is bounded on the outside by the mantle-like layer consisting of small cells, on the inside by the white germ-cells (z). In this lower portion, however, the mantle is much thicker than above, where it forms the cover of the cavity of segmentation. In other words, the subdivision of the large germ-cells into smaller cells has progressed in this region toward the axis of the egg. All that lies on the outside of this fissure is no longer the analogue of the sensorial layer (Remak), but contains the rudiments for all germ-layers. From the fissure there is developed later a portion of the visceral cavity, and what now lies to the outside of the fissure will subsequently constitute the entire thickness of the back. In sufficiently thin sections, made from preparations that have been hardened in chromic acid, it is possible to distinguish in this part of the back two very distinct layers of unequal width. The external thinner layer consists of small cells and is the analogue of the sensorial layer (Remak); the internal thicker layer consists of larger cells, which, however, are considerably smaller than the large germ-cells in the centre of the bottom of the cavity of segmentation. This inner thicker layer splits up later into two layers, the innermost of which is composed of single cells (intestinal and glandular layer, Remak), while the other represents the middle or motorial and germinative layer, which is here pretty strongly developed.

Fig. 426.

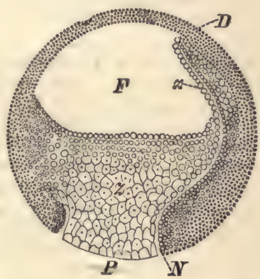

Fig. 426. A vertical section passing through a great circle of the egg of Bufo cinereus. For the sake of clearness the cavity, which extends from N to beyond Z, has been drawn throughout its whole length as a broad fissure, while in reality this is only true of its upper half. D, cover; Z, bottom of the cavity of segmentation, F; P, small white area beneath.

The deposit of cells (z), which in section appears sickle-shaped, increases steadily in an upward direction towards the pole; at the same time the (in a horizontal section) semilunar fissure keeps pace with it in its upward progress. Owing to the fact that the fissure penetrates between these newly deposited cells, a portion of them on the outer side of the fissure remains attached to the cover of the cavity of segmentation as a permanent deposit, while the other portion (D), which is at the same time the thinner of the two, remains as a septum between the fissure and the cavity of Von Baer.

If meridional sections be made through eggs which have reached the stage of development we are now discussing, in such a manner as to divide the dorsum into two halves (fig. 427), it will then be seen that those cells which extended from the bottom of the cavity of segmentation up on to its cover and remained adherent to this cover after the formation of the semilunar fissure, lead in a downward direction to those cells which were previously described as belonging to the thicker inner layer of the lower portion of the dorsum. In other words, that portion which subsequently became adherent to the cover of the cavity of segmentation is the foundation for the motorial and intestinal and glandular layers.

I have already stated that the original cover of the cavity of segmentation represented only the analogue of Remak's sensorial layer. This layer

now is composed in the Batrachia, as Van Bambeke* and I† have both shown, of two thicknesses: the one superficial, consisting of a single layer of brown cells; the other deeper in, consisting in some places of a single, in others of a multiple layer of whitish cells. The outer brown cells constitute the foundation from which the horny coverings of the animal are developed, while the inner whitish cells serve to form the sensorial layer proper.

Fig. 427.

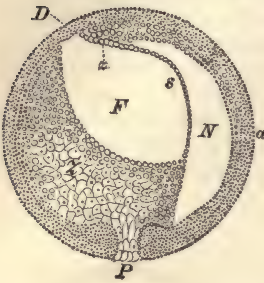

Fig. 427. This illustration, which has already once been published, was drawn by me in 1860, from a remarkably successful preparation. I am unable now to say to what extent I was at that time diagrammatic in filling in the finer details of the drawing. In the main features, however, I drew it as truthfully as possible. I therefore do not hesitate to make use of this drawing again, even though since that time the same relations have been illustrated in a beautiful manner by Götte Van Bambeke and Golubew. My drawing, it appears to me, renders the subject much easier to understand; and, after all, this is the main thing. *D*, *F*, *P*, *Z*, *z*, the same as in fig. 426. *a*, dorsum of the embryo; *s*, boundary between the food-cavity (*N*) and the cavity of segmentation.

In Birds and Mammals both of these thicknesses are so intimately united together that even in the very best transverse sections a differentiation is impossible. For this reason Remak has looked upon them both as a unit, and has termed the entire layer "sensorial layer" (central portion) or "horny layer" (peripheral portion). In so doing, however, he has given expression to the theoretical doubts which must arise against the supposition that the horny and nervous elements both originate from the same layer. All the more interesting therefore is the circumstance that in the Batrachia, and also—as I shall show further on—in Fishes, horny and nervous elements are found distinctly separate, even in the first stages of development. Bearing these relations in mind, I shall designate the external brown layer of cells as the *horny layer*, and the deeper whitish layer of cells as the *nerve layer*. In the case of Birds and Mammals, however, and, in fact, wherever else further investigations may be needed on this point, I shall designate the external germ-layer (Remak) as the *united horny and nerve-layer*.

If we recapitulate briefly the results of our description, it will be remembered that the horny and nerve layers originate in an external mantle-like zone of the spherical egg, while the motorial and glandular layers originate in the large germ-cells which are collected together as a reserve stock in the lower half of the egg. The germ-cells carry out this metamorphosis in part directly, in the spot where they lie (lower half of the egg), in part, however, after first being displaced, either actively or passively. The direction of this displacement is from what was originally the lower pole to the upper pole, or—which means the same—from the tail to the head of the future larva.

As soon as the Rusconian furrow becomes a complete circle, there is also developed from its abdominal half a fissure which grows in the direction of the upper pole. This fissure, however, scarcely attains one-fourth of the

* "Recherches sur le développement du Pelobates brun" (*Mémoire publié par l'acad. Belgique.* Tome 34).

† Loc. cit.

height of the collection of germ-cells, and, at the blind end of the egg, it broadens out somewhat. (These dimensions will of course vary considerably in the different species.) Remak has named this fissure the "anal cavity."

The first fissure, which is situated in the dorsal half, and is semilunar in shape when seen in transverse section, is completed by the anal cavity. If we now carry a horizontal section through the egg near the level of the lower pole, there will be displayed to view a fissure with circular outlines. Close to the lower pole this circle becomes somewhat narrower, and finally terminates at the exposed Rusconian furrow. Here then we have a funnel-shaped space, commencing at this furrow and giving lodgment to the plug, which is composed of white germ-cells (Ecker's vitelline plug). By the gradual narrowing of the canal, in which the outermost portion of the plug lies, the white field becomes so small as to be recognizable merely as a whitish point. Even this, at a later date, disappears, and there is then left a canal which can be recognized only in sections and by the aid of a powerful magnifying-glass, and which has been termed unanimously by all authors the *anal opening*. Owing either to the retrocession of the greatly diminished plug of white germ-cells, or to its becoming broken off—an undoubted occurrence in Bufo cinereus—the Rusconian cavity thenceforth communicates with the anal cavity throughout its entire breadth. A small ring-shaped pad, visible with the naked eye on the outer wall of this cavity, still marks the place where formerly the vitelline plug obstructed the cavity, and the depression in the pad affords a good landmark to guide us in making the section—where our object is to hit the mouth of the canal.

Fig. 428.

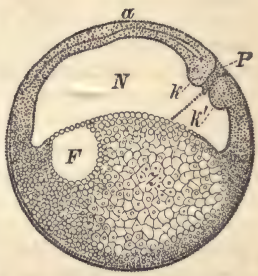

Fig. 428. *F, N, a, P, Z*, the same as before; *KK'*, section of the circular pad and confines of the anus; the dotted line indicates the former connection between the vitelline plug and the mass (*Z*) of germ-cells; at this stage the egg has already completed its partial revolution, thereby causing the back to lie above, and the belly below.

In the mean time the egg has performed its partial revolution, the meridian has become the equator, the anal opening lies at one side, the dorsal half is above, and the ventral half, together with its mass of germ-cells, protruding very markedly into the food-cavity, is below. A trace of Von Baer's cavity of segmentation usually remains for a long time in this mass of cells.

From this time on the egg can be considered as a vesicle surrounded by walls or laminæ of several thicknesses, and modified by the circumstance that in the lower half of the vesicle the innermost layer is lifted up by the subjacent mountain of germ-cells. As a rule, however, the different layers are not in all places of the same thickness. But at this point I must break off with the description, for the variations just alluded to constitute the beginning already of the foundation of the organs, which cannot be described in this place.

B. Fowl's germ. In the Fowl's egg the germ consists of the so-called Cock's-tread, which in company with the yellow yolk is enclosed in a common membrane. Pander * described the Cock's-tread as consisting of two easily distinguishable portions, one of which dipped down into the yellow of the egg, while the

* *Beiträge zur Entwickelung des Hühnchens.* Würzburg, 1817.

other was spread out like a layer over its surface. The latter, he says, is a round disk, in and from which the fœtus is formed, and which, therefore, may very properly be termed the *germ-membrane.* The other portion Pander called the *nucleus of the Cock's-tread.* It is a component part of the so-called white yolk, and lies beneath the central transparent portion of the germ-membrane, though not connected with it.

The doctrine enunciated by Pander, that the embryo is formed exclusively from the germ-disk, remains even to the present time unshaken in its foundations.

Reichert * and His,† judging from different stand-points, have, it is true, supposed that the formed elements of the white yolk entered into the new body of the animal. His, moreover, on the basis of this supposition, has designated the germ-disk as the *principal germ* (Archiblast or Neuroblast), and the portion contributed from the white yolk as the *subordinate germ* (Parablast or Hæmoblast). These views, however, are not sufficiently supported by facts, and it will be seen farther on, in the course of my description, that the observations which gave birth to these views will admit of another interpretation, conformable to the general principles of biology.

Pander's description relates to fructified eggs taken from under a setting Fowl, before they become hatched. The commencement of hatching, however, must not be considered as in any sense the commencement of development. The processes which are of the most importance for our description take place on the passage through the oviduct. It is there, for instance, that segmentation of the germ takes place, and that the elements of segmentation begin to arrange themselves in layers. In the hatching egg the disposition into layers is found to have attained different degrees of advancement in different cases; it would, therefore, on this account alone, be unadvisable to attribute a definite histological character to this period.

The segmentation of the Fowl's germ was first described by Coste.‡ His description, however, embraced only what could be seen by simple observation of the surface of the germ-disk, during the process of segmentation. Oellacher§ examined sections of Fowls' germs in the various stages of segmentation, and in his treatise we find for the first time a description that corresponds with the conditions as really observed. I must therefore first give an account of this description. Inasmuch as Oellacher's investigations were carried on under my special notice, my description will also in part be based upon personal observations.

All the preparations mentioned here were obtained in the following manner: The yolks of eggs, taken either from the oviduct or from under a setting Hen, during the first day of hatching, were carefully freed from albumen and washed cautiously in dilute chromic acid; the precipitates of albumen, thus produced, were then removed by the forceps, and the cleansed yolk again placed in a fresh dilute solution of chromic acid. At the expiration of a few days the segment of the yolk, in which the germ-membrane is visible, should be lifted off and carefully placed in alcohol: here it is to remain until deprived as thoroughly as possible of its water, and then it should be embedded. For this purpose a small paper box ‖ must first be prepared and then half filled with a mixture of wax and oil. When the mixture in the small box has stiffened to such an extent that we may be confident that a preparation laid upon it will not sink to the bottom, then place the specimen in the desired position on the semi-solid mass, and fill the box full with the fluid mixture. As soon as the second portion commences to stiffen, the position of the preparation should be accurately noted, so that

* *Entwickelungsleben im Wirbelthierreiche.* 1840.

† *Untersuchungen über die erste Anlage des Wirbelthierleibes.* 1868.

‡ See his "*Histoire du développement des corps organisés.*"

§ Stricker. Stud., 1870. ‖ See Addenda.—TRANSLATOR'S NOTE.

when the mixture has become solid a line may be drawn indicating the direction in which the section is to be made. The wax and oil should be mixed in such proportions that the consistency of the mixture, when stiff, shall be suited to the consistency of the preparation and the individual notions of the investigator. I cannot avoid the present opportunity of expressing my astonishment at the obstinacy with which skilled microscopists refuse to avail themselves of the advantages which the mixture affords. The mixture of two substances of such different consistency as wax and oil enables us to obtain all the different degrees of consistency between both of them separately. For the extremely delicate embryological preparations these advantages are invaluable.

I will also cursorily remark that, if the preparation contains cavities, these must be opened in order that the mixture may fill them completely. It is only when the preparation and the wax mixture are in the fullest contact that we can expect to obtain good sections.

The little paper boxes should be of such a size that the investigator can hold firmly in his hand the solid mass therein moulded. The knives used in making the sections should be large, of the highest degree of sharpness, and ground flat at least on one side; the upper surface of the blade, furthermore, should be covered with a coating of oil of turpentine. After completing the section the preparation should, by the aid of oil of turpentine, be floated off on to the slide, where it can be mounted permanently according to the ordinary method (oil of cloves, Damar varnish, and a wall of paper).

So far as the real topographical relations can be ascertained from sections through eggs hardened in chromic acid, the fully matured germ displays the form of a biconvex lens, which at one pole—in the natural position, the under one—is somewhat depressed. The diameter of the germ measures about 0.5 mm.; its thickness between the depressed portions is 0.05 mm.; between the biconvex portions, 0.06 mm. In a body like this the spot where the germ is to be sought for is marked out very distinctly. Above it lies the vitelline membrane, while beneath it is a finely granular mass, concerning which it cannot at this stage be determined whether it belongs to the germ or not. In this stage Oellacher was not able to discover a germinal vesicle in the sections.

The first furrow of the germ was found in an egg which—according to the time usually occupied by the Hen in laying an egg—had yet from 12 to 14 hours to spend in the oviduct. The body interpreted to be the germ occupied a situation similar to the one before described, but was rather larger and thicker. From the centre of the convex surface of the germ, a tortuous line of subdivision of the substance pursued a somewhat oblique course downwards.

A view of the second phase in the process of segmentation was obtained in an egg whose shell already contained lime salts in a sufficient quantity to admit of demonstration. In the spot where the germ is to be sought for, there was again visible an approximately concavo-convex disk; it appeared thinner, however, and larger than that of the previous stage. In this case five furrows penetrated from the surface into the substance of the disk, so that when seen in section it appeared to be subdivided into six fields; of these the two outermost were the longest, while the four middle ones did not vary materially from each other in their dimensions.

At this period also it was impossible to determine positively whether beneath these fields other subdivisions of the germ, though perhaps not quite so sharply outlined, did not exist.

A view of the next stage was obtained in an egg whose shell was already hard, though relatively very thin. Here there existed already a distinct division between the germ and the yolk, for an appreciable cavity separated the two. A section through the middle of the germ showed that it was composed of polygonal fields, of which as many as six could be counted in passing from the surface down to the cavity.

The shape of the germ as a whole—and we could speak positively concerning its shape, owing to the fact that its lower boundaries were so sharply drawn—always approximated to that of a bi-convex lens, whose upper surface lay in immediate contact with the vitelline membrane, while its uneven under surface formed the upper boundary of the shallow cavity separating the germ from the yolk. The largest fields occurred at the borders and were filled with larger granules than in the middle parts. In some of the fields a nucleus was distinctly visible.

In a later stage—which was also observed in an egg taken from the oviduct—the process of segmentation was found to have advanced much further. The larger polygonal fields were only present along the borders. In the central parts the formed elements were smaller and more loosely joined together; their contents, moreover, in the upper layers were finely granular, but in the lower layers they became coarser. Throughout the peripheral portions, the germ-disk lay upon the yolk; in the central portion, however, the two were separated from each other by an intervening shallow cavity. At the bottom of this cavity lay a few formed elements, similar in their external appearance to those composing the deepest layer of the germ-disk.

A still later stage of an oviduct-egg presented but few features worthy of mention. The process of subdivision had made still further progress even along the borders: the formed elements in general were smaller, the entire disk was somewhat thinner, the cavity deeper, and at the bottom of it lay a few large, spherical, strongly granular formed elements. Finally, in another oviduct-egg a still later stage of development was found. The elements of segmentation—the embryonic cells, we can also say—were in some spots separated into two layers; in the upper layer (*S*, fig. 429) the cells were small and closely packed together, whereas in the under one (*D*) they were larger, more coarsely granular, and arranged with great irregularity, forming in certain spots a simple row, in others, again, small heaps (on transverse section), of two or three cells in depth, by whose accumulation projections were produced.

In freshly laid eggs the germ is sometimes no further developed than what we have just described, while at other times the under layer, which is composed of larger cells, is more sharply separated, throughout its whole extent, from the upper layer.

We may say in general that in freshly laid eggs the separation of the germ into two layers is at one time more, at another less pronounced, but that the process of segmentation will be found to have not yet entirely ceased. The formed elements of the under layer are still pretty large: a few very large segmentation-spheres (*M*, fig. 403) may even yet be found projecting prominently downwards into the cavity, or sometimes even resting upon the bottom of the cavity, so that in transverse sections the germ-membrane appears as if supported upon pillars. Occasionally these large elements are found lying on the bottom of the cavity, without touching the germ-membrane above. In such cases it will of course remain doubtful whether these elements became detached during life or through the action of the reagent employed. At the same time the appearance of larger and smaller elements, like these lying on the bottom of the cavity, is an affair of such constant occurrence that one cannot avoid the conclusion that they must either have fallen down already during life, or have remained lying there after the removal of the germ-membrane.

Near the free border the germ-membrane is thickened by the presence on its under surface of large segmentation-spheres; from this point on, how-

ever, it rapidly diminishes to a thin edge. The last-mentioned thickening rests upon the yolk, so that the entire germ may be said to lie like a cover over a shallow depression in that body. The cavity resulting therefrom was called by Remak the "germ-cavity." The wall limiting the cavity His termed the "germ-wall." This wall, however, is not a part of the germ: it belongs to the yolk, and therefore its designation as germ-wall is inconsistent with the facts.

Fig. 429.

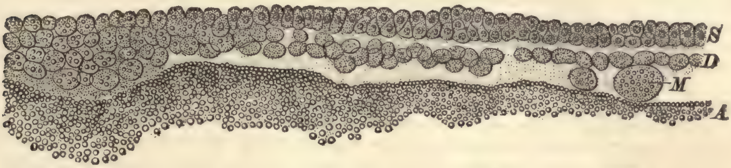

Fig. 429. Section of the germ of an egg freshly laid in the month of June.

Inasmuch as the descriptions of embryologists refer also to the stage last discussed, it would be the proper thing here to give a sketch of the literature of the subject.

The prevailing doctrine concerning the development of Vertebrates from the so-called germ-layers owes its origin to Caspar Friedrich Wolff.* From him we learned that the entire complex intestinal system is developed from a simple laminated foundation-work.

Pander † perfected Wolff's theory. The germ-membrane, according to him, consists of a layer of granules, constituting the foundation from which later the under germ-layer will be formed. Above this layer, furthermore, there will be developed, during the first hours of hatching, a second layer of similar granules—the subsequent upper layer; consequently, about the twelfth hour of hatching the germ-membrane will be found to consist of two laminæ, the upper one of which he calls the *serous*, the under one the *mucous lamina*. Although he likewise describes the middle layer as the vascular layer, yet his description in this part lacks clearness; at times, for instance, he describes the layer as a fully formed mass in which vessels become developed, then again he represents it as the result of the development of the vessels. Nevertheless he clearly understood the fact that after hatching had continued for a period of twenty-four hours, three easily separable germ-layers could always be found in the germ-membrane. Pander moreover was the first person who attempted to draw up a general plan of development for the organism. He attributed to the upper germ-layer the origin of all those organs, which since the time of Bichat and Reil have been termed *animal*—namely, the nervous system together with the organs of sense, also the muscular and osseous systems; the middle layer he considered to be simply a vascular layer; while the under layer, according to him, serves as a foundation for the intestinal system, together with its accompanying glandular organs.

The investigations of Von Baer ‡ were connected with those of Pander and may be considered as a continuation of the same. Von Baer describes in the unhatched egg a single layer—the rudiment of a germ-layer. He states, furthermore, that during the first hours of hatching a second layer is formed, not *above* the first-mentioned layer, as Pander holds, but under it, and that it constitutes the groundwork of the under germinal layer. Von Baer gives the same description as Pander of the middle germ-layer (vascular layer). Von Baer's general plan of development was also more perfect than those of his predecessors. He demonstrated the fact that the middle germ-layer participated in the formation of the fibrous groundwork of the intestine and glands belonging to it. According to him the two layers, which originated during the first hours of hatching again subdivide each into two layers, the upper ones forming the *cutaneous* and *muscular plates*, the under ones the *mucous* and *intestinal fibrous*

* De formatione intestinorum, 1768–69. Deutsch von Meckel, 1812.
† Loco citato.
‡ *Ueber die Entwickelungsgeschichte der Thiere*, 1822, I.

plates. The two upper layers together he called the *animal layer*, while both lower ones he designated as the *vegetative layer.* Reichert * gave still a different interpretation to the affair. He distinguished in the germ-membrane of the impregnated but unhatched egg a layer of bodies, from which during the first hours of hatching a membrane (enveloping membrane) becomes developed. The formation of this membrane was considered by Reichert as a necessary forestep to the further development of the embryo, inasmuch as from its inner side the yolk-cells are produced and deposited there in layers. At first the foundation for the nervous system is formed, then that of the middle layer, which, owing to its situation between the upper and lower germ-layers, he designated as the membrana intermedia. When the formation of this membrane is completed, the development of the under layer commences by an accumulation of yolk-cells upon the under surface of the former : this takes place at a time when the embryo is already beginning to become separated from the germ-membrane by the process of constriction. As regards the significance of the germ-layers in the subsequent development of the embryo, Reichert held that the upper layer takes no part in the formation of the embryo itself, but ceases to live during the embryonic life of the organism. In reference to the middle layer, moreover, he was the first to prove the subdivision of the side plates and the participation of the middle layer in the formation of the walls of the trunk. The horny layer of the skin, the cutaneous glands, the muscular, osseous, and vascular systems, as well as the intestinal fibrous membrane with the glandular organs belonging thereto, are also developed, according to him, from this layer. The under layer is described by him as simply furnishing the groundwork for the development of the epithelium in the organs of digestion.

Remak was the first to speak of the germ membrane, in the impregnated though unhatched egg, as consisting of two layers. The next changes then, according to this authority, take place in the under layer : it becomes more compact, though still looser in texture and less transparent than the upper. Then follows a histological differentiation of its elements : a layer of cells becomes detached and lines the under surface like an epithelium. As regards the relation of the germ layers to each other in the region of the area germinitiva (Fruchthof), the upper and middle ones appear, at a very early date, to be thickened and mutually adherent at the centre of the area. The under layer, however, does not form adhesions with the others in this place. Excepting in the middle portion of the area germinitiva, all three layers can be easily separated from each other throughout their entire extent. Having ascertained the anatomical individuality of the germ layers, Remak further endeavored to establish their relation to the different organs, during the subsequent development of the organism. The names which he has given to the layers are of themselves a sufficient explanation of this relation. He calls the upper layer—as already stated—the *horny* or *sensorial layer*, the middle one the *motorial and germinative layer*, and, finally, the under one the *intestinal and glandular layer*, owing to the fact that from it is developed the epithelium of the intestinal system with its appropriate glandular organs.

His† again described, in the fructified though unhatched egg, only a single layer of bodies (constituting the foundation-work for the upper germ-layer (archiblast or neuroblast). According to him the under layer is developed, during the first hours of hatching, by a lengthening and fusion of the (subgerminal) processes, which project from the under surface of the upper layer, and consist of one or several rows of cells. In other words, the under layer is from the very start a production of the upper. From these two layers, according to His, is formed the entire embryo, with the exception of the system of blood-vessels and the group of connective substances, both of which are formed from the so-called white yolk. He taught, furthermore, that in the central portion of the area germinitiva, a layer separates itself from the upper germ-layer, and one also from the lower; finally, that an axial cord of connection is formed between the upper and lower germ-layers.

Hensen‡ states that the separation of the germ-membrane into germ-layers takes place at a later date than was supposed by Remak. He describes, furthermore, in that period of the development of the embryo in which the chorda dorsalis manifests itself in the centre of the area germinitiva, a "special membrane, firm and non-nucleated," to which he has given the name of "membrana prima." It is situated between the upper and middle layers, lying closer to the upper than to the lower, and has important bearings, according to Hensen, upon the development of the embryo.

* Loco citato. † Loco citato.
‡ Virchow's *Archiv.* Bd. xxx. Max Schultze's *Archiv.* Bd. iii.

According to Dursy,* the middle portion of the germ-membrane, the embryonic plate, is composed of two laminæ at about the fifteenth hour of hatching; of these laminæ he interprets the under one to be the foundation from which the subsequent middle germ-layer is formed. He maintains that Remak's supposition, that the middle layer is produced by subdivision of the under layer of the germ-membrane, has not yet been proved. The under layer, he says, perhaps becomes developed later from the yolk.

Waldeyer,† again, sided with Remak, in so far as the latter taught that the middle germ-layer and the intestinal and glandular layer were developed from what was originally the under layer. Still Waldeyer, independently of Peremeschko, recognized the fact that a large part of the cells which are subsequently found in the embryonic mass arrive there by wandering between the germ-layers. In regard to the cells, however, which are found at the bottom of the germ-cavity, Waldeyer was unable to decide whether they were segmentation-spheres or products emanating from the white yolk. Moreover, what His called "subgerminal processes," he did not consider as products of the upper germ-layer, but as primary offshoots from the egg-cells.

As the statements of Peremeschko‡ and Oellacher § form the basis of my own description, I shall omit them.

By comparing my description with the historical sketch above, it will be seen that my interpretation of the germ-disk in the freshly laid egg is the same as Remak's, namely, that it is composed of two laminæ. I would further add that the separation between the laminæ is not a perfect one throughout the entire extent, for there are sometimes places where the two still adhere closely to each other; it is only after they have been subjected to the heat of incubation that the separation becomes complete.

The cells of the under layer change their form and arrangement during the first hours of incubation. They become flattened, and, when seen in transverse section, appear spindle-shaped (*D*, fig. 430). Hence after incubation has gone on for a few hours, we can ascertain, beyond even the shadow of a doubt, from thin transverse sections of well-preserved specimens, that there are two, and only two layers: the upper layer is thicker, more compact, and has a depth of two to three, or even more cells; while the under layer consists of a number of flattened cells, which in transverse section appear spindle-shaped. The under layer, immediately after its separation from the subdivided germ, consisted in some places of a single thickness of cells, while in other places, in a transverse section, small heaps of cells could be recognized projecting from the layer. What became of these heaps of cells in the mean time, I am unable to say.

Peremeschko, however, has made the communication that the large granular cells, lying on the bottom of the germ-cavity, increase very considerably in numbers during the first hours of incubation. Now, since with this increase in numbers there is not at the same time a corresponding diminution in size, it is very natural to suppose that the cells which project from the under germ-layer fall to the bottom of the cavity. This supposition, moreover, appears all the more probable, when we recall to mind the fact, mentioned in a previous part of our description, that some of the elements of segmentation, which are situated in the lower portion of the germ, remain lying at the bottom of the cavity at the time when the germ, in the production of this very cavity, separates itself from the subjacent parts.

According to my description, therefore, the under one of the two original layers is not identical with the layer described by Remak under the same name. From this under layer, according to Remak, are separated, by splitting, the middle layer and what becomes subsequently the under layer. In

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* *Der Primitivstreif des Hühnchens.*

† *Zeitschrift für rat. Med.* 1869.

‡ *Wiener Sitzungsberichte*, 1869.

§ Loco citato.

point of fact, however, the process is different. The original under layer consists—at least above the germ-cavity, and before the middle layer has made its appearance—of only a single stratum of flattened cells, and it retains this structure for still quite a time after the formation of the middle layer. The much thicker middle layer cannot originate, by splitting, from this stratum of flattened cells.

Peremeschko has seen the first traces of the middle layer at about the seventeenth hour of incubation. It must be remembered, however, that the number mentioned here is only approximately correct, for allowance must be made for the degree of temperature employed in hatching,* and the condition of the egg at the commencement of the process. With this reservation I append the statements of Peremeschko.

At about the seventeenth hour of incubation there appeared between the upper and lower layers coarsely granular elements, which, in respect to size and contents, differed materially from the cells both of the upper and under layer, but yet were the same, to all appearance, as those lying on the bottom of the cavity; soon afterwards the central groundwork of the middle layer was formed. In some preparations it was noticeable that this groundwork consisted in part already of the cells which characterize the subsequent middle layer, in part still of the characteristic large, coarsely granular elements (*M*, fig. 430); the upper layer appeared to be separated from the layer in question by pretty sharp limits. *The central portion, then,*

Fig. 430.

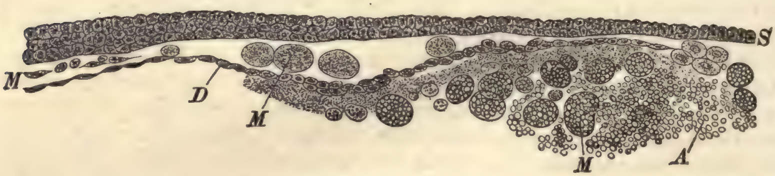

Fig. 430. Section through the Fowl's germ (first day of hatching).

of the middle layer became developed earlier than the other parts of the layer. Preparations in which the central portion was already developed, displayed on both sides of it, as far as to the periphery, and even a little beyond it, in the space separating the upper and lower layers, newly-formed cells, characteristic of the middle layer: they occurred in the form of thin laminæ or small groups, and sometimes among them were scattered the larger, coarsely-granular elements; in certain spots these last could also be seen in a state of transition to groups of cells. From this observation it may therefore be assumed that the middle layer is developed from the large, coarsely-granular elements.

During this process of development of the middle layer we notice that the formed elements, collected in large quantity in one spot (bottom of the germ-cavity), gradually diminish in bulk, while elements that look just like them make their appearance in an adjoining space (between the upper and under layers), increase in number, and become transformed into groups of smaller cells.

* In hatching I make use of a water-bath which is kept at a temperature of 39° Cels. (circa 102° Fahr.), by means of a self-regulating gas flame.

We are consequently led to conjecture that the process is one of translocation; that the granular bodies, which before lay at the bottom of the cavity, have found their way to the space between the two first germ-layers.

At about the twenty-third hour of hatching all three germ-layers were fully developed. The cells of each layer bore such characteristic features that they could easily be distinguished one from the other. Mention was made above concerning the cells in the upper and under germ-layers: those of the middle layer were small round cells, with extremely delicate outlines and oblong, sharply defined nuclei.

The relation of these layers to each other is such that it is possible to demonstrate them as separate objects, excepting in the middle portion of the germ-membrane, where the middle layer is inseparable from the upper. The large elements, which have frequently been spoken of as lying on the bottom of the cavity, were studied by Peremeschko as to their behavior upon the heated slide.* They change their form at a temperature of 32°–34° C. (circa 90°–93° Fahrenheit). This change in form commonly consists at first in a general shrinking, which can be inferred from the circumstance that they diminish in size and become opaque; their shape at the same time becomes oval or round, with irregular edges; afterwards they increase in size, and again become more transparent. This phenomenon of distention and contraction was repeated, in one specimen, several times. He observed the changes in form, both in hatched and unhatched eggs, but they took place very slowly.

Peremeschko's observations were afterwards confirmed by Oellacher. I had the opportunity of seeing the different appearances bearing on these points so often that I can testify to the truthfulness, in the main, of their statements.

By comparing the arrangement of the elements of segmentation in the Batrachian and Fowl's germs, the following facts are ascertained: The outer germ-layer or Remak's sensorial layer in the Batrachia is divided into two strata, while in the Fowl's germ it remains single; in both cases, however, it originates from a superficial layer of cells which had subdivided earlier than the deeper layer; from this latter originate the other two layers, the under and middle layers. In a certain stage, then, there are found lying opposite to each other in both germs an upper layer of small cells and an under one of large cells.

In the Batrachia, as well as in Fowls, the larger cells (which subdivide more slowly) experience at first a partial dislocation within a cavity which becomes developed during the progress of the segmentation: in the Batrachia it is the large germ-cells that push their way up over the inside of the cavity of segmentation; while in Fowls it is the large, coarsely granular elements which at first fall to the bottom of the cavity, and then, in order to get between the upper and under layers, must wander thither either actively or passively. In both cases the slowly subdividing, large elements form the foundation of the middle and glandular layer; it is only in regard to the mode by which they accomplish this that differences of opinion exist. In the case of the Fowl we know that with the formation of the first deposit the middle layer has not yet reached completion. I will show later that during the second day of development there occurs a second immigration of large, coarsely granular elements, destined to lay the foundation from which the vessels are to be formed; I would mention, however, in passing, that

* See introduction.—TRANSLATOR'S NOTE.

the supply of these large elements at the bottom of the germ-cavity was not exhausted by the first emigration.

In the Batrachian eggs we find no analogue for this subsequent completion of the middle germ-layer by the accession of a special deposit for the blood-vessels. The reason for it, however, lies in the fact that nothing is yet known concerning the first rudiments of blood-vessels in these eggs. At all events, after the formation of the middle layer, there is also left behind, in the Batrachian egg, a supply of large elements of segmentation (fig. 428), concerning whose destiny we as yet know nothing.

C. Trout's germ. In the interest of comparative anatomy, I will also communicate in brief the facts that have been ascertained concerning the embryonic layers in Osseous Fishes. Rynck * studied this question on Trout's eggs under my immediate observation, and his communication is the only one that is founded on data from sections. From it we learn that the subdivided germ † lies upon the yolk throughout its entire extent at first, but that afterwards, while the germ spreads itself out, there is formed the cavity which Lereboullet ‡ has already made known to us. This cavity is in every respect the analogue of the germ-cavity in the Fowl's egg. The germ is stretched out over the cavity, its thickened edges lying upon the yolk at the periphery of the cavity. The portion stretched out over the cavity shows also in its under layer larger cells, which are arranged here and there in small projecting heaps, exactly as is the case in the Fowl. Little by little the under surface becomes even, and the portion lying above the cavity is then found to be composed of two strata, each consisting of equally small cells. The upper stratum is formed of a single row of cells, while in the lower stratum they are found two or three deep. Further investigation revealed the fact that from these two strata is developed only the analogue of Remak's sensorial layer. Hence this layer is composed, as in the Batrachia, of two separate deposits (Anlagen).

Upon the bottom of the germ-cavity lie large, coarsely-granular elements. The source from which these elements came can hardly be disputed. The yolk of the Trout's egg contains no formed elements from which they might be derived. Consequently there is no other explanation left than that they are portions of the subdivided germ which, during its separation from the subjacent yolk, either remained lying upon the latter or afterwards fell down there from the under surface of the germ. The relations, therefore, which exist here, in and about the germ-cavity, are analogous to those which we found in the Fowl's germ.

In the mean time more characteristic differences are developed. To render these clear, I must first notice certain comparative embryological relations. Coste § has already called attention to the fact that the embryo of the Fish is not placed in the axis of the germ, as is the case in the Fowl, but in a certain part of the thickened border. The following description will enable the reader to understand readily the relations under consideration. In the first place, let us imagine a small sphere of wax placed upon a larger one of wood, and the first flattened down upon the larger in such a manner as to resemble a disk with thickened borders; the flattening should then be carried still farther, until the thickened border, which in the mean time has steadily increased in extent, encircles the equa-

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* *Max Schultze's Archiv.* Bd. V.

† The process of segmentation was first described by Rusconi, in the year 1836 (Müller's *Archiv*).

‡ *Nouvelles recherches et Annales d. sc. nat. Zoolog.*, II., 1864.

§ Loc. cit.

tor of the sphere of wood. The cap of wax should now be stretched beyond this point, until the thickened border, which is thereby rendered thinner, becomes reduced down, in the neighborhood of the pole which lies opposite to the starting-point of the process, to a very narrow, barely visible ring. The sphere of wood is now almost completely covered by the cap of wax. Precisely similar are the relations between the germ and the yolk in the Trout's egg. By hardening the eggs in chromic acid at various stages of development, and lifting off carefully the thick vitelline membrane, it is possible to demonstrate to the naked eye the different degrees to which the enveloping growth has advanced. Before the cap has covered the first third of the vitelline sphere, it will be noticed already that the thickened border is particularly thick in one spot. With an ordinary magnifying-glass there can be made out in this spot the dorsal furrow, which lies in the direction of the upper pole (in the original position of the germ).

During the extension of the cap this rudimentary deposit grows in the form of a thickened cord of the cap, which starts from the thickened border and pursues its course in the direction of the upper pole. When the border has finally become reduced to a narrow ring, scarcely visible to the naked eye, this cord stands related to the embryo in a manner which reminds one strikingly of the relation in which the Rusconian anal opening of the Batrachian egg stands to the axis of the dorsal half. Rusconi also called attention to this resemblance.

The dorsal furrow in the Batrachian egg stretches from the anal opening toward the upper pole, but does not, however, reach it. In exactly the same manner is the thickened cord, which represents the dorsum of the Trout's embryo, related to the ring-shaped remainder of the thickened border, which, as is well known, encloses a canal. Through this canal, in the Trout's egg, the yolk lies exposed to view, while in the Batrachian egg, where there is no yolk, large segmentation cells appear.

Of the rest of the cap the smaller part is converted into the sides of the body, while the larger part forms the vitelline sac.* The centre of the germ disk, which, of course, lies originally above the germ cavity, constitutes in the Fowl the most important portion—that is, the embryo proper, while in the Fish's egg it is simply the rudiment of the vitelline sac. In both germs the cells which are underneath fall to the bottom of the germ cavity. In the Fowl, however, there remains behind a stratum, which constitutes later the intestinal and glandular layer. In the Trout the cells all fall down, so that no foundation is laid in the centre for a glandular layer.

If, while the thinned centre (S) of the germ (which has not yet spread itself out over an area of much extent) is still suspended above the cavity, we trace the large cells (M), which lie on the bottom of the cavity, out toward the periphery, we shall notice that they are directly continuous with a deeper layer of large cells, which, at the thickened border, constitute the under layer, and, as will be seen farther on, furnish the foundation work not only for the motorial layer but also for the intestinal and glandular layer.

This condition of things suggests the idea that the large cells at the bottom of the germ cavity wander toward the periphery, there either to form or to reinforce the deposits of large cells which are found in that region. It must be remembered, however, that beneath the walls of the vitelline sac a rich network of blood-vessels is developed, and that it is perhaps in this

* See my illustrations in the *Sitzungsberichte der Wiener Akademie*, Bd. LI.

direction that the large cells, which lie upon the bottom of the cavity, find their ultimate destination.

D. Mammals. I have myself made comparatively unimportant observations on the first changes in the Mammalian germ. In this department, therefore, I am simply a compiler. Notwithstanding the value of the literary material at my disposal, I am unable to make use of it except to a very limited degree. This is owing to two reasons: in the first place, because I cannot give in this place a history of the discussions through which the first firm principles became established; in the second place, because during the most recent epochs of embryology the Mammalian egg has not been studied at all.

Fig. 431.

Fig. 431. Section of the germ of Salmo fario.

The earlier communications on this subject do not accord well with the newer forms of belief, and I have no inclination to harmonize these incongruences on paper. I prefer to present the statement with all its imperfections, calling attention, however, to the fact that in the history of development of the Mammalian egg there are many treasures yet to be disclosed.

Bischoff was the first to give a definite description of the process of segmentation in the Mammalian egg. Although he himself* gives Karl Ernst von Baer the credit of the first acquaintance with the process, I cannot as a historian agree with him; Bischoff's own description is in reality the first. It stands at the height even of our present views on the subject. We find it clearly stated there that the germ (vitellus) subdivides, within the membrane and independently of it, into smaller formed elements. While now the germ (vitellus) of the Rabbit's egg—so it reads in the original treatise—is still in the very process of subdividing into smaller and smaller spheres, the egg itself, surrounded by a thick layer of albumen, escapes from the oviduct into the uterus. According to the concurrent testimony of De Graaf, Cruikshank, Coste, Wharton Jones, Barry, and Bischoff, the egg occupies pretty constantly 2½ days in its passage through the oviduct.

Bischoff's drawings, which inspire us with a sense of their truthfulness, lead us now to conjecture that even the Mammalian egg does not subdivide uniformly throughout its whole extent. Within the uterus there is also developed in the Mammalian egg a cavity, which gradually increases in size in such a manner that the elements of segmentation, crowded toward the periphery, surround the cavity in the form of a very thin layer, or, as it is also expressed, they constitute the wall of a vesicle. In this condition the ovule had already been seen by De Graaf. He described it as a vesicle composed of two membranes. The outer membrane is, as Bischoff represented it quite clearly, the germ envelope, while the inner constitutes the germ membrane proper. Bischoff also described a dark mass, which consisted of spherical bodies and lay next to the inner surface of the germ-vesicle, though at no

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* *Entwickelungsgeschichte des Kanincheneies.* 1842, p. 66.

special part of it. These are spherical bodies, said he, which quite resemble the spheres resulting from the previous subdivision of the germ; in fact they are clearly the same elements. These spheres, then, in the process of segmentation must have been left behind, resting against those cells which constitute the extremely thin and at this time very clear and transparent vesicular wall. The question, whether the point at which these germ cells are massed is identical with the spot where later the germ vesicle manifests a thickening of its substance, must be postponed, at least for the present.

At this thickened spot (Von Baer's *germ hill*, Coste's *embryonic spot*) Bischoff first discovered a splitting into two layers, and his description of this spot corresponds exactly with the relations we have in recent times and by the aid of better means of investigation ascertained to exist in Birds, Batrachia, and Fishes. According to that description the cells of the animal layer constitute a dense membrane, while the cells of the vegetative layer appear still distinctly separate, very delicate, and pale. I would not attempt to decide how at the present time these two layers are to be interpreted. A single tolerably clear section from a Bitch's egg of the same age led me to consider the two layers of which the germinal vesicle, outside of the rudimentary dorsum (germ hill), is composed, as the analogues of Remak's sensorial and glandular layers. A more definitive elucidation, especially of the relations which exist in the germ hill, is left for the future.

I am unable, at the present time, to give any further information about a third vascular layer (whose existence Bischoff took for granted, and of which much has been said in the literature of this subject) that is found between these two layers. In the first place, it is doubtful whether this middle layer is really a vascular layer, or corresponds to Remak's middle germ-layer. In the next place, the question of the development of the middle germ-layer in Mammals demands a new and thorough investigation. After what has been ascertained by comparative-anatomical investigations in other orders, I would not venture to reproduce any of the views published hitherto. As regards the fact that this layer also contains vascular rudiments, I shall recur to it farther on.

E. Morphological Value of the Germ-Layers. As regards the external germ-layer, it has been mentioned already that it contains the rudiments of the central nervous system, of the nervous constituents of the organs of sense, and of the superficial cellular covering of the animal. Furthermore, an explanation has been given why I term it the combined horny and nervous layer. In the Batrachia, in which the horny layer is distinct from the nervous layer, the relations are remarkably clear. The horny layer is uniformly thin throughout its entire extent, and first becomes thickened at the spot where the well-known *suckers* of the larva originate. From it originate the internal cellular lining of the central canal, the outer cellular covering of the animal, and the cellular lining of all glands pertaining to the latter. As regards the nervous layer, however, I have found it, even in the earliest stages, thickened in that part where later the brain is developed. From here it tapers down gradually toward the tail end (vitelline plug), but somewhat rapidly in all other directions.

There is no special thickening corresponding to the rudiments of the retina, for it, as is well known, is developed from the brain (by the sending out of a diverticle-like process). Special thickenings* exist, however, for

* See the treatises of Schenk and Török in the "Wiener Sitzungsberichten," Bd. L. and Bd. LIV.

the organs of smell, taste, and hearing. As to the rudiments of the organ of touch, I am unable to state anything; I must draw attention, however, to the fact that the nervous layer, like the horny layer, surrounds the entire periphery; investigations should therefore be made as to how this peripheral expansion is related to the organ of touch.

In spite of Remak's positive assertions, I am unable to consider the question settled as to whether nervous elements may also be developed from the middle germ-layer. Concerning this point, further and very thorough investigations are needed. Observations on the tail of the Frog's larva render it probable that the peripheral nerves originally grow from the axis to the periphery in the form of protoplasma processes. But, wherever these processes once penetrate, there, and in any part of their course, cellular elements may become developed from them. So long, then, as this theoretical consideration is not overthrown by positive observations, we are not justified in considering this important question as settled according to Remak's views.

From the middle germ-layer are formed the muscular and connective substances. It is so easy to prove this assertion by observation, that I do not consider it necessary—although influential voices have been raised against it—to make it the subject here of a prolonged discussion.

In the first place, the dorsal cord belongs to the connective substances. The most primitive section, however, teaches that the cord involves the entire thickness of the middle germ-layer; that above, it terminates at the central nervous system; while below, it ends in the glandular layer. From those portions of the middle germ-layer which bound the cord laterally, are developed in pairs the vertebræ. Again, the most primitive sections teach that these vertebræ, as Remak has already shown, become separated into distinct subdivisions. Only a part of each primitive vertebra becomes bone; another part certainly becomes muscle, and it is supposed that a third part forms the rudiments of the skin.

I have shown,* furthermore, that in that spot where later the front part of the cranium originates, bone and muscle are formed by the development of boundary-lines in a matrix which was originally uniform in appearance; here, also, then, there can exist no doubt concerning the genesis, of the connective substances.

Reichert, as already stated, first recognized the splitting of the middle germ-layer to form the pleural and peritoneal cavities. With the present method of studying the history of development from sections, the recognition of these relations has become a comparatively easy matter. It will be seen that the parts bordering on the sides of the vertebræ (side-plates, Remak) subdivide, exactly as described by Remak, into two layers, between which the serous cavities are developed. The lining, therefore, of these cavities is formed, beyond all doubt, from the middle germ-layer. As to the remaining details, I would refer the reader to Remak's clear account, according to which the upper of these two layers attaches itself to the combined nervous and horny layer, while the under one unites with the glandular layer, to form, on the one hand, the abdominal walls, on the other, the intestinal canal. In the former case, the horny layer furnishes the external cellular covering, and the cellular lining of the external glands; while in the latter case, however, the intestinal and glandular layer provides the cellular lining of the intestinal cavity, as well as of all the glandular organs which grow out from the intestine.

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* Archiv von Reichert und Dubois. 1864.

The relations of the first rudiments of the urogenital apparatus to the middle germ-layer have already been described by Waldeyer, on page 528.

Formation of the Simple Tissues in the Embryo.

Very little is to be added to what I have already said (page 45) concerning the formation of cells. Since that time I have devoted more attention to the subject of cell-division, and have found that the process may be observed with comparative ease in inflamed tissues. The only precaution required is to keep the tissues, while we are studying them, under conditions which favor the continuance of life.* In this way direct observation has demonstrated what, upon theoretical grounds, seemed long ago to have been decided. At the same time, it has been shown that the old diagram was not quite correctly drawn. It is not necessary that a cell should first become biscuit-shaped † before it can undergo subdivision. It subdivides either during active amœboid motion, by the separation of the cell-body into two masses connected together by a thin thread, which eventually breaks; or, the cell assumes the shape of a more or less spherical mass, in which a line of subdivision becomes visible; sometimes this line disappears and returns several times in succession, until it finally becomes permanent. In these cases, direct observation affords us a satisfactory proof of the actual subdivision only when one or both parts resume their amœboid motions, and become completely separated from each other. As a rule, however, the cells do not separate from each other; they subdivide, and the cementing substances between them alone indicate the separation which has taken place.

By the investigation of the proliferation of cells in inflamed tissues the cell-theory has experienced a certain modification. It has been ascertained that cells which have already attained such an age that amœboid motions can no longer be perceived in them (fixed connective-tissue corpuscles), may under favorable influences, inflammatory irritations and their results, again become amœboid. It has been ascertained furthermore that this does not hold good for old cells in general. It also happens sometimes that the external layer of the cell remains unchanged, while only the central portion recedes from its surroundings; the cell is converted into a bladder in which one or several amœboid cells lie.

In this way it is shown that the explanation given by Brücke of the endogenous formation of cells (page 45) harmonizes very completely with the processes as they actually take place. Oser's ‡ observation, that the cells formed endogenously escape through rents in the maternal envelopes, settles the matter effectually.

After the explanations given in this (first) chapter, no further elucidation is needed concerning the development of the epithelia and endothelia.

The development of connective substances has been discussed by Rollett in the second chapter of this work. I would only remark, as this seems to be the proper place, that I consider the formation of fibrillated connective tissue from cell-processes as proven. On the other hand, I do not consider it as strictly proven that a homogeneous basis substance splits up into fibrillæ.

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* Stricker, Studien aus dem Physiol. Institut.
† The shape of a "lady-finger" (cake.)—TRANSLATOR'S NOTE.
‡ Stricker, Studien aus dem Physiol. Instit. p. 83.

Our knowledge of the first rudiments of embryonic blood-vessels relates almost exclusively to the Fowl's germ.

We find that even C. F. Wolff was acquainted with the fact that in the germ disk of the Fowl the blood originated in the form of islands, and Pander penetrated still farther when he showed that the Wolffian blood islands were formed of smaller dark islets, which could be distinguished both in the transparent area and in the opaque zona. Pander said that these islands lengthen themselves out and grow narrower, their ends interlock, and thus there is formed a reddish network with transparent interspaces. Von Baer made mention, though in a very obscure manner, of Pander's islets; but later these observations of Pander's were consigned to oblivion. After the publication of Remak's investigations, people very generally adopted the views of this observer, who mistook a secondary stadium for the primary, but at the same time interpreted it in a very comprehensible manner. Remak mistook the completed network of blood-vessels for the first rudiments of the system, and, inasmuch as he saw them at the same time filled with blood, he gave the following explanation of these appearances:—Cells unite to form trabeculæ and plexuses, and the peripheral elements of each cord form by fusion the walls of the vessel, while the central elements become blood corpuscles. When therefore a few years later the silver method revealed the cell-limits even in the capillaries, Remak's theory seemed to be more firmly established than ever.

It was only a few years ago that Affanasief* again discovered the insular rudiments of the blood-vessels. In this instance I must make an exception, and state that his work was carried on under my direction. I do so because Affanasief afterwards declared that what he had found was indistinct and unsatisfactory—a point on which I must differ from him. Soon afterwards His also declared himself in favor of the island-shaped rudiments of the vessels, and very recently E. Klein† has at last given us satisfactory results concerning this question. The points which still remained obscure in Affanasief's account are thereby rendered perfectly clear. I shall therefore enter now upon the description of the primary development of blood-vessels with the consciousness that I am treating of a topic which, from a morphological stand-point, is definitely settled.

If a fresh germ disk be examined at the beginning of the second day of hatching, with moderately strong magnifying powers and without a glass cover, there will be observed in the deeper parts of the tissue isolated cellular elements in various stages of development into large, bladder-shaped bodies provided with vacuoles. In an optical transverse section, the large bladders appear to be composed of spindle cells. During the development of the cell into a bladder, the nuclei in the wall of the bladder increase in number and project inwards toward the cavity; there appear moreover to be as many spindle cells in an optical transverse section as there are nuclei visible. Klein has shown that cells are separated from the inner wall of these bladders by the process of constriction, and that these cells fall into the cavity of the bladder and become blood-corpuscles.

The isolated cellular elements may also be recognized in sections of hardened preparations. In examining such sections it will be seen that these elements, for reasons already previously brought forward and discussed, must be considered, like the cells of the middle layer, as products of the subdivided germ which subsequently find their way hither by wander-

* *Wiener Sitzungsberichte*, 1866. Bd. LIII.

† *Wiener Sitzungsberichte*, 1871. Märzheft.

ing. It will be seen furthermore that from their definitive location they should be reckoned as belonging to the middle germ layer. We see therefore that from a segmentation sphere or an embryonic cell there is developed a bladder containing blood-corpuscles, or, as we may also term it, a vessel built after the type of capillary vessels and closed on all sides. The wall of the bladder is protoplasm, whose nuclei have multiplied, and the enclosed cavity has originated in the same manner as vacuoles are usually produced.

The blood-corpuscles are produced within the cell endogenously. This takes place, according to Klein's description, by the protrusion from the inner wall of the bladder of buds, which become disconnected by constriction and fall into the cavity of the bladder. There is also a second mode of endogenous blood formation, which stands more nearly related to the endogenous cell-formation with which we are already familiar. The central portion of a large cell sometimes becomes transformed into blood corpuscles, thus presenting the picture of a cyst filled with blood-corpuscles. Both forms are fundamentally the same; in both cases they are closed vessels which contain blood-corpuscles and which have originated from single cells.

From the walls of such bladders shoots grow out which at first are solid but afterwards become hollow. Furthermore, the free end of a shoot may develop into a bladder of one form or the other, so that then we shall have two cysts which communicate with each other; or, the shoots of different bladders unite; or, again, a shoot forms a junction with a bladder, or two bladders communicate directly. In this way a communicating vascular system is formed. The formation of shoots continues on after the completion of a communicating network. In the tail of the Frog's larva, where the new formation of vessels may be observed at a time when the circulation is already established, the formation of shoots is so sharply pronounced that the most conservative observer cannot fail to recognize them. The walls of the vessels send out processes, the processes become thicker and unite either with the processes of other vessels or with the vessels themselves directly, and a communication between the two is established by the hollowing out of the processes. At the same time there is also a probability that even in the tail of the Frog's larva free cells develop outrunners, attach themselves to a vessel, and then play the same rôle as that just described in speaking of the vascular outrunners. The observation made by me * that spindles, closed at both ends and containing blood-corpuscles, occur in the tail of the Frog's larva, has been recently confirmed by J. Arnold. † These observations suggest the idea that an endogenous formation of blood takes place even in the tail of the Frog's larva. Moreover it has already been determined, by investigations which are still going on in my laboratory, that in the so-called vascular centres of inflammation (vascularisirenden Entzündungsheerden) blood can be formed endogenously by the transformation of cell walls into walls of vessels. No other mode of new formation of vessels has hitherto been observed.

Originally all vessels, whether they form later the heart, arteries, or veins, are constructed like capillary vessels, that is, they possess only a nucleated wall, which in the embryonic state consists of embryonic cell-substance or protoplasm. The complication which afterwards takes place in the structure of the heart, arteries, and veins, is the result of a secondary process in the outer wall of the original tubular system, concerning which more accurate

* *Wiener Sitzungsberichte.* Bd. LII.

† Virchow's *Archiv.* Bd. 53.

information has not yet been furnished. The endothelia of the heart, arteries, and veins possess therefore the same genetical dignity as the walls of the capillaries.

Inasmuch as in the capillaries of the completed vascular system there can be brought out by the silver method a system of brown lines which are directly continuous with the brown lines of the cementing substance of the endothelial cells lining both the arteries and the veins, we must assume that the lines of cementing substance throughout the entire system were formed afterwards. This course of things is in harmony with the general principles of development. With the exception of the first rudiments of the middle germ layer, no other example is known of the coming together of cells to form a cellular structure. In all the epithelia as well as endothelia we see the process of cell subdivision manifesting itself only to the extent that from a single cell two or more cells may be formed; these last do not, however, separate from each other, but cementing materials make their appearance, which indicate the lack of continuity of the individual cells. We must assume that exactly the same thing takes place in the originally homogeneous tubes of protoplasm. In this connection I would again employ an example I have already used (page 49), *i. e.*, that the vessels are originally constructed like gun-barrels with smooth bore, but that afterwards they appear like the shaft of a chimney.

As to the question of where and how the blood is formed in the embryo, after the completion of the first rudiments of the vessels, we possess, indeed, very little knowledge. Reichert* has expressed the view that the blood is formed in the liver. No satisfactory proofs, however, have been brought forward in favor of this view. Neumann's and Bizzozero's † theory concerning the formation of the blood in the early stages of the embryo must also be discarded, for bones provided with medullary spaces only make their appearance at a later period. The question still remains unanswered whether the medullary spaces in the fœtal bones ever serve as centres for the formation of blood, and if so, at how early a stage. Finally, for the early stages of development the lymph glands can hardly be looked upon as the source of the colorless blood-corpuscles, for, as Sertoli ‡ has shown, the first traces of these corpuscles are first met with in embryos of a later period of development.

Before describing the development of the transversely striated muscular fibres, I must make some additional remarks on their structure, especially as in this particular the description in chapter VI. is incomplete. The transversely striated muscular fibres are spindle-shaped or cylindrical, with blunt or pointed ends. The thickness of the fibres is very variable: sometimes they may be recognized with the naked eye, while at others they are very much thinner. In a small muscle the fibres are as long as the muscle itself, but in the larger muscles they do not exceed 4 centimetres in length.

Schwann discovered a sheath—the sarcolemma—surrounding the muscular fibres, and since that time it has been customary to consider this sarcolemma as entirely filled with the muscular substance proper. In fresh fibres the sheath is invisible, but it can be seen if we treat the muscular fibres with water or with dilute acetic acid—in short, with reagents which leave the sheath intact, but cause the muscular substance to swell; the sheath bursts then at some point, the muscular substance protrudes, and in such cases the outline of the rupture in the sheath can be pretty distinctly recognized. It is sometimes possible in such preparations, especially if we do not employ

* *Entwickelungsgeschichte*, etc. † *Entwickelungsleben*, etc.
‡ *Wiener Sitzungsber*. Bd. LIV. 1866.

fresh muscular tissue, but that which has been dead about twenty-four hours, to render the sheath visible over tracts of considerable extent. We recognize it then as a very thin, extremely transparent, and, as it appears with the means of observation at our command, structureless membrane.

Schwann also discovered the nuclei of the muscular fibres; these are the muscle-corpuscles of the authors, by an exact study of which Max Schultze, as is well known, gained the first foot-hold for the reform of the cell-doctrine. Often, if not always, a border of finely granular substance is seen around these nuclei; hence, in these cases the muscle-corpuscles are cells, consisting of cell-body and nucleus.

The muscle-corpuscles generally lie on the surface of the muscular substance, between it and the sarcolemma. Donders * has found that in the muscular fibres of the heart the muscle-corpuscles lie within the substance of the fibre. Rollett † has shown, furthermore, that muscle-corpuscles are found within the substance in the muscles of Amphibia, Fishes, and Birds.

Schwann finally represented the muscular substance as composed of fibrillæ, which he compared to a string of pearls. He attributed the peculiar appearance, by reason of which these fibres are commonly designated as transversely striated, to the regularity with which the thinner and thicker fibrillæ were placed alongside of each other. If, for instance, we look at the surface of such a fibre, we shall notice, as a rule, light and dark zones of a certain breadth, which alternate with each other. These zones, therefore, are said to owe their origin to the regular manner in which the thick and thin sections of the fibrillæ are placed side by side. Hence a muscular fibre consisted, according to Valentin, of a bundle of fibrillæ, and since that time it has also been called a primitive muscular bundle.

Bowman believed that the fibrillæ were not originally present in the fibre, but were the product of a degenerative process. He stated that the fibres sometimes break up, not in the direction of their length, but in that of the transverse striations, thereby causing the production of disks. Furthermore, he believed that by splitting a muscular fibre in both directions—that is, lengthwise into its component fibrillæ, and transversely into disks—we should obtain minute subdivisions—"sarcous elements," which are the real constituents of the muscular fibre. Rollett called attention to the fact that Bowman had only spoken of one kind of substance, and had overlooked the cementing substance.

Wharton Jones, however, was the first to make mention of the alternation, in the longitudinal direction of the fibres, of two different substances, *i. e.*, of disks and an intermediate substance.

Dobie went a step farther and described the fibrillæ as being likewise composed of two different substances, which gave to the fibrilla the appearance of a linear row of alternating bright and dark bodies. Rollett accepted this description. He believed that the muscular substance of the fibre consisted (Schwann's view) of a bundle of fibrillæ, and considered each fibrilla as composed of an alternating series of two substances, to one of which, on account of its sharper outlines, he attributed a greater power of refracting the light than the other. The more strongly refracting substance he called the *principal substance*, the other the *intermediate substance*. In the case of the entire fibre, disks of intermediate and principal substances alternate with each other, the latter corresponding to the disks of Bowman. In the case of the individual fibrillæ the principal substance corresponds to a

* Physiologie des Menschen; deutsch von Teile.

† *Wiener Sitzungsberichte*, 1857.

sarcous element or fleshy particle. Rollett was able even at that time to give information concerning Brücke's discovery, which revealed the fact that the characteristic of double refraction belonged only to the principal substances, but was wanting in the intermediate substances.

In respect to the internal arrangement of the fibrillæ Rollett was led, by the study of transverse sections from frozen portions of Oxen's hearts, to adopt Leydig's views, according to which the primitive muscular bundle is traversed by a system of cavities. He drew this inference from the configuration of the designs observed in the transverse sections. By macerating the sections for several days, he also obtained a view of the fibrillæ in transverse section. Later, Cohnheim * reduced the freezing of fresh muscular fibres to a method, and demonstrated that transverse sections of muscular fibres thus frozen must be considered as transverse sections through a living tissue. From these sections he ascertained that the muscular substance proper was composed of two entirely different substances: one very transparent and brilliant, the other only slightly transparent and of a dull appearance. These two substances were distributed unequally in bulk. The brilliant substance he described as a close lattice-work of narrow lines, which become broader only in a few places and intersect at all possible angles; while the dull substance is arranged like a mosaic, in the form of countless small three-, four-, and five-angled figures, which are separated from each other by the narrow seams of the more transparent substance. In a few spots he found the corpuscles composing the mosaic separated farther apart, and the brilliant substance accumulated in greater abundance: in the midst of such spots the muscle-nuclei were visible. Cohnheim considers the dull fields of the mosaic as transverse sections of the sarcous elements. He states furthermore that the transverse section of the living muscular fibre corresponds to the longitudinal section to this extent, that in the latter the sarcous elements are also visible, surrounded by a second different substance. In regard to the consistency of the sarcous elements, Cohnheim, relying on the investigations of Kühne, states that it must be that of a fluid.

This description led to a materially new interpretation of the muscular structure. According to it the muscular substance proper is composed of sarcous elements, surrounded by an intermediate fluid substance and arranged in layers (disks) like the courses of building-stones in a wall.

Kölliker † opposed this view of Cohnheim's; he believes that the fields described by Cohnheim are the transverse sections of muscular pillars, which in turn are composed of smaller bundles of fibrillæ. He therefore interprets the transverse section in the same manner as Leydig and Rollett.

From the description on page 154 of this book it may be inferred that Kühne interprets the contents of the muscular fibre in the same manner as Cohnheim.

These, then, were the prevailing views up to the time when the works of Krause and Hensen, which appeared nearly simultaneously, threw a materially new light upon the case. According to Hensen,‡ the muscular fibres are constructed somewhat as follows:—

In the primitive muscular fibre, when in a state of rest, every transverse band is found to be subdivided by a dark line into two halves. This line marks the location of a delicate disk (middle disk). Hence, in a muscular fibre there is not simply an alternation of a strongly refractile substance—

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* Virchow's *Archiv*, Bd. 34.

† See his "*Handbuch*," 1867, and "*Zeitsch. f. wiss. Zool.*" Bd. 16.

‡ *Arbeiten aus dem Kieler physiologischen Institut*, 1868.

the transverse disk—with one that is feebly refractile—the intermediate substance, but the first half of the transverse disk is followed by a feebly refractile substance—the middle disk; then comes the second half of the transverse disk, and finally the intermediate substance.

Krause's * view is different. According to him each muscular spindle, leaving out of the account the sarcolemma, consists of a very large number of muscular caskets. Each muscular casket contains a muscular prism, which consists of the anisotropic substance which almost completely fills the muscular casket. The form of the muscular prisms (sarcous elements) is that of a many-sided column, cut off transversely above and below; while the transverse diameter varies, the height of the muscular prisms, like that of the muscular caskets, is almost constant throughout the entire series of Vertebrates. Both end-surfaces of the prism are covered by a thin layer of fluid (fluid of the muscular caskets). Between [the ends of] every two muscular caskets there exists a basis membrane, which separates the caskets from each other. Each casket, moreover, possesses a membrane of its own, which completely envelops its sides and becomes fused with the two contiguous basis membranes. In the transverse direction of the muscular spindles the caskets are arranged in uniform disks, which may be termed muscular compartments. Each compartment consists of a basis membrane, which in profile appears like a line, transversely directed; then follows, as we look along the muscular spindle, one of the halves of a clear transverse band, then a dark transverse band, then the half of the clear transverse band next in order, then again a transverse line, and so on.

The most striking difference between Hensen's and Krause's interpretations of the appearance noticed, lies in the fact that Krause considers that as a muscular prism—consequently an anisotropic portion—which Hensen interprets to be intermediate substance and isotropic portion.

Heppner † raised doubts concerning Hensen's and Krause's views. He believed that the brilliant zones (Krause's fluid of the muscular caskets, Hensen's transverse disks) were simply a manifestation of the total reflection that takes place at the boundaries between the principal and the intermediate substance. He was confirmed in this view by the circumstance that the position of the brilliant bands, relatively to the boundary layer which separates them (middle disk, Hensen; transverse line, Krause), can be changed by shifting the position of the mirror, or the bands may even be made to disappear altogether, when the mirror is placed in a certain position. The appearances noticed when polarized light was used still further confirmed him in this belief. For instance, if we color the field of vision by the aid of scales of mica, it will be seen that the shining bands as well as the dull disks always appear of the same color. Hensen and Krause assumed, however, that only one of the two was anisotropic.

So far as the interpretation is concerned, which Krause and Hensen have given to the appearances first noticed by them, I must range myself on the side of Heppner. At the same time I do not wish to intimate that the question is at all settled. Since the time when Heppner made the researches referred to above in my laboratory, I have made frequent and thorough investigations on the structure of the muscular fibres, but have not been able as yet to come to any conclusion as to the question under consideration.

* *Zeitschrift für Biologie*, Bd. 5.
† *Max Schultze's Archiv*, Bd. 5.

My researches were made exclusively upon fresh muscular fibres which were placed upon the slide and covered with a thin glass cover, without the addition of any fluid; slight pressure was then exerted upon the edges of the glass cover, which rested upon narrow ridges of putty. Moreover, I made use chiefly of the muscles of the Hydrophilus, notwithstanding the fact that Hensen had so strongly denounced their use in a subsequent publication against Heppner: I did so because the muscles of this animal, as skilled microscopists have already noticed, are peculiarly favorable for our purposes of investigation.

If our examination be made with a Hartnack's lens, No. 15, we shall perceive, in those cases where the still living muscular fibres appear striated transversely, that the intermediate substances (in Rollett's sense of the term) are not homogeneous. If they be not too narrow, we can distinctly perceive that dark granules are lying here in a clear basis substance. In the direction of the length of the fibre I have very often been unable to count more than two granules in a disk. As a rule, the arrangement of the granules in the clear basis substance varies. At one time the entire intermediate substance appears like a densely granular zone of protoplasm; at another it is free from granules in certain spots, or they are sparsely and irregularly distributed throughout the substance. It has often been stated that by changing the focus the intermediate substance will appear at one time clear, at another dark. I must, however, state very positively that, with the definition which lens No. 15 gives, the intermediate substance, when in exact focus, is always dark in that part where the granules lie, but that, where no granules exist, it is always clear, in fact clearer than the principal substance. The principal substance retains a uniform dull appearance under all changes in the focus.

The microscopic appearance presented by the muscular fibres of the Hydrophilus, so long at least as their motions are very active, are exceedingly variable. In those which appear to be only transversely striated, the breadth of the principal and intermediate substances changes, and the form of the boundary surfaces of both varies, so that the intermediate substance at one time presents the appearance of a knot, at another that of a constriction; furthermore, the position of the disks varies relatively to the vertical position: at one time they are warped, at another they are even and vertical. Each particular zone, moreover, does not always include the entire surface or the entire area of a section; dislocations sometimes occur; in such cases one-half of the fibre may be dislocated upon the other to the distance of half a disk's breadth; at the same time the boundary outlines between the principal and intermediate substances may be interrupted or bent at an angle. Other fibres appear transversely and longitudinally striated; the longitudinal striation at one time passing through both substances, at another being confined to the principal substance alone. Again other fibres appear only longitudinally striated, and others still are neither transversely nor longitudinally striated. There is no doubt, however, that all these conditions belong to living fibres. The wavy motion may be seen with great distinctness in a fibre which is neither longitudinally nor transversely striated; it may also distinctly be seen how such a fibre will suddenly take on, throughout its whole extent or only in spots, the most elegant transverse striation, and then afterwards with equal suddenness lose it. I can only compare this condition of things to the picture presented by a corps of infantry actively engaged in performing their evolutions, when seen from an elevated position: at one moment it presses forward in more or less deep columns, and seems to be composed of transverse brand of

unequal breadth; the next it forms again into lines which stand at right angles to the direction of the column; and, finally, it forms a quadrangle, in which transverse and longitudinal striations disappear at one moment, and then, in the next, either one or the other of them reappears. It is clear that such manifestations accord best with the idea according to which the muscle is composed of small groups of disdiaclasts and a fluid intermediate substance. At the same time we must not at present close our eyes to the fact that many doubts may be raised against this way of viewing the matter.

It seems to me important to mention also those researches which relate to the muscular tissue of the lowest forms of animals. Perhaps the researches made in this department will some day settle the questions more decisively than is possible by investigations among the Vertebrates and Arthropods. Inasmuch as I have made no investigations myself in this field, I shall have to follow the latest publication on this subject, namely, that of Schwalbe;* I would also recommend the perusal of this work to all those who are anxious to become better acquainted with the subject and the literature belonging to it. The following points, which are of general importance, are the only ones I shall take from this account:—The Cœlenterata are the lowest form of animals in which transversely striated muscular fibres can be found. Max Schultze, Brücke, and Virchow have seen distinct transverse striations in the muscular fibres of the swimming-disk of Aurelia aurita, and Kölliker in the fibre-cells of Pelagia and Agalmopsis. Furthermore, according to the observations of Schwalbe in Ophiothrix fragilis (Echinoderms), the muscular cells between the ambulacral vertebræ possess in the first place a sarcolemma, and in the next place the muscular substance appears to have double oblique striations. From his account similar systems of lines have before been observed by Mettenheimer in the muscles of Arenicola piscatorum and Nereis succinea. Mention is also made of the same appearances in the description of the Mollusks. Another important point, which was observed particularly in the muscles of the Nematoda and Hirudinæa, is that the fibre-cells are composed of two substances, a medullary substance surrounding the nucleus, and a cortical substance which may be decomposed into fibrillæ. This observation was made by G. Wagener on cross-sections of dried muscular fibres from Aulosdoma nigrescens. Schwalbe corroborates the observation on Hirudo medicinalis. These observations appear to me to be especially important, because they indicate a stage of development in Vertebrated animals. Finally, I would call attention to the fact that Weissmann † has subdivided muscular fibres into muscular cells and primitive muscular bundles, a subdivision opposed by G. Wagener.‡ Wagener held that the fibrilla was the primitive element of muscular fibres.

In respect now to the development of muscular fibres, I can state the case in a very few words. So far as I have been able to judge from my own investigations on embryos of the Rabbit, I must side with Remak and those who are of the same mind with him in the view that a muscular fibre is developed from a cell, which in the first place assumes the shape of a spindle and increases in thickness; the nuclei then multiply, and on their outer surface is developed a mantle of longitudinal striations, which mantle serves at the same time as the cortex for a nucleated and granular medul-

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* Schultze's *Archiv*, Bd. 5.
† *Zeitschrift für rationelle Med.* 1862 and 1864.
‡ *Archiv* von Reichert, etc. 1863.

lary substance. When once this mantle is formed, fibres will also soon be met with, in which the mantle is likewise transversely striated. It would appear then as if each spindle cell became converted gradually into muscular substance, in the direction from the periphery toward the centre. It is important to mention that the first trace of muscular substance in the fibre cells appears always to be a fibrillation. It should also be mentioned, however, that we cannot examine such fibres in an entirely fresh condition. If we remove them from living embryos, they very soon die; hence it still remains undecided whether the muscular substance at its first appearance really is fibrillated. In regard to the formation of the sarcolemma, I must state that I was unable to find, in the course of its development, any points which would justify me in considering it as a cell-membrane. On the contrary, I have made observations which render it very probable that the formation of the sarcolemma is to be referred to cells, which attach themselves to the muscular cell in such a manner as to surround it like a sheath. If for instance we examine a specimen of muscle taken from the muscles of the trunk in a Rabbit's fœtus, and prepared by simply tearing it apart, we shall find that the muscular fibres, about the time when they are not yet fully devoloped, and are therefore still either homogeneous in appearance or else consist of cortex and medulla, lie embedded in heaps of small cells; we shall find, furthermore, among the isolated fibres some to whose outer surface more or less prominent nucleated cells are attached. It can also be seen how the body of such a cell, in an optical longitudinal section of the fibre, spreads itself out along the edge of the fibre in the form of a thin, extremely transparent band, presenting the appearance of a section of the sarcolemma. In view of the interpretation now given of Schwann's sheath, and also in view of the circumstance that Schwann's sheath and the sarcolemma are sometimes continuous the one with the other, it is not improbable that the latter is formed from cells which have placed themselves in apposition with the surface of the muscular fibres. It should however be borne in mind now that those muscular corpuscles, which are found between the sarcolemma and the muscular substance proper, may very well owe their origin to the cells we have just spoken of. This view is confirmed in the first place by the circumstance that the nuclei of the young muscular fibres are situated in the medulla; secondly, because the cortex of the muscular cells is converted into muscular substance proper; and finally, in the third place, by my observations of the relation of the embryonic muscular cell to the smaller cells which attach themselves to its surface. According to this view, then, the superficial muscular corpuscles of the sarcolemma should perhaps be interpreted as connective-tissue corpuscles. I must however embrace this opportunity to state again that the connective substances and muscular tissue are to be referred genetically to one and the same source, and furthermore that it will not do to draw the conclusion from my view of the superficial muscular corpuscles, that these latter are incapable of taking part in the regeneration of muscle.

In regard to the development of nerve tissue it is only quite recently that we have received definite information through the investigations of Babuchin.*

* It was a part of the original plan of the editor to publish the discussion of this question in connection with the description of the electrical organ. Prof. Babuchin undertook this task, and made several visits to the coast of the Adriatic for the purpose of carrying on the investigation. This year however Babuchin found it necessary to visit Egypt for the same purpose. Inasmuch as it would hardly answer to put off the completion of the manual until the time of his return, the editor prefers

The results of his investigations * show that no essential difference exists between the minute structure of axis cylinder processes and other processes of nerve cells. Embryonic cells are the best objects in which to satisfy one's self that the axis cylinder process has no connection either with the nucleus or nucleolus. The embryonic nerve cells, which already possess fully developed axis cylinder processes, are provided with a very large nucleus, which at first sight appears to be naked, and to be situated directly upon the end of the axis cylinder, like the head of a pin upon the shaft. On closer examination, however, and with a good magnifiying power we can appreciate the fact that the large nucleus is surrounded on all sides by a very narrow, sharply outlined layer of protoplasm, which is continuous with and constitutes the commencement of the axis cylinder. At its commencement the axis cylinder is conical in shape and comparatively thick, but farther on in its course it grows narrower, usually without subdividing, and passes into an uncommonly thin fibril. In this condition it passes out from the cranial cavity of the embryo, and extends even to the remotest portions of the same, where it not unfrequently breaks up into a bundle of extremely fine fibrils, scarcely visible with any degree of distinctness except with a Hartnack's No. 15.

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to close the work with the material already at hand. The investigations of Babuchin will appear as a separate pamphlet, of the same size as this book.

(Prof. Stricker writes, under date of June 14th, 1872, that Prof. Babuchin's work is not yet ready for publication.—EDITOR.)

* *Centralblatt*, 1868.

SUPPLEMENTAL ARTICLES.

I. On the Structure of the Synovial Membranes,

By Dr. EDWARD ALBERT.

We observe that as early as the times of Bichat, that author separated the synovial membranes from the serous membranes proper and grouped the former in two classes, viz. :—

1st. The capsules of the tendinous sheaths (synovial capsules); and, 2d, the synovial membranes of the joints.

Since that time no effort has been made by anatomists to attack this classification, and the aim of experiments has been merely to discover whether an epithelial covering similar to that of the synovial membrane investing the joints existed also on the articular cartilages. It was only in the year 1866 that Hüter * published a work, the results of which seemed almost to exclude the synovial membranes from the position which had so long been claimed for them in the catalogue of Human membranes.

Guided by the results of the silvering method, Hüter denied the existence of an endothelium, and claimed that the synovial membrane was provided externally with a peculiarly modified connective tissue, the forms of which sometimes remind one of endothelium, at other times of the serous canaliculi in the cornea (epithelioid and keratoid connective tissue). The opposition which Von Recklinghausen's method met with from Schweigger-Seidel † extended also to the views maintained by Hüter, while Schweigger-Seidel based his chief argument in favor of an epithelium upon the regular arrangement of nuclei on the surface.

Landzert, in a late publication, has been still more determined in maintaining the existence of an epithelium (endothelium) above the outlines of the serous canaliculi. On the other hand, Böhm, ‡ in his inaugural dissertation, accepts all of Hüter's views with regard to the tracings in the synovial membranes, as brought out by the silver method, and still further extended them, for examination of a fresh specimen, in a solution of common salt, led him to believe that the innermost layer of the synovialis was a layer of non-nucleated cells. §

If we take whole joints, open them freely, and immerse them for several days in a solution of chromic acid (1 part to 10,000, or perhaps 5,000), we find little difficulty in bringing into view complete cells on the innermost layer of the synovial membrane. These cells are made still more distinct when slightly tinged with carmine, and are then observed to form a continuous layer, being rounded or polygonal in form, some provided with very short outrunners, but every one of them having a well-defined granular nucleus, which is rounded or oval. The nucleus sometimes fills almost the entire body of the cell, so that a narrow border is all that remains to be seen of this substance; in some cases the nucleus is centrally situated and is smaller, while the cell-body is larger.

By this method of investigation it was ascertained with certainty that the innermost layer of the synovial membrane is completely invested with nucleated cells.

It is very remarkable, further, that in silver preparations we detect two

* Virchow's *Archiv*, Bd. 36, and Klinik der Gelenkkrankheiten, 1870.
† *Arbeiten aus der physiologischen Anstalt zu Leipsig*, 1860.
‡ *Centralblatt für medicinische Wissenschaften*, 1867. No. 24.
§ *Beiträge zur Anatomie und Pathologie der Gelenke*, 1868.

series of tracings over extensive portions of the synovial membrane. The figures seen in the upper layer correspond quite closely with the outlines of endothelium. The underlying layer shows the characteristic vascular network, with long, rhomboidal, and square meshes, the serous canaliculi being intermediate.

In comparing this view of the case with Hüter's, the difference most difficult to reconcile appears to be as to the figures resembling epithelium, which Hüter* says seem to lie in the same layer with the keratoids (serous canaliculi).

If, however, we have convinced ourselves in successful preparations that this is not universally the case, then we are readily tempted to regard Hüter's views as erroneous (Landzert), and to hold the synovial membranes for simple serous membranes. But as we proceed further in our investigations, it becomes more apparent that the superficial irregular (keratoid) tracings cannot be the outlines of ill-formed endothelium, and it becomes clear that though figures resembling endothelium occur throughout the greater portions of the synovial membranes, still in certain places they are uniformly absent, and for those places Hüter's statement is doubtless true.

In what special localities this occurs may be stated in a general way, as for instance: If we take the highest point of an articular head of bone, taking, for example, the head of the humerus, and regarding it as a pole, we find about it round cartilage-cells which in Adults are separated from one another by broad bands of intercellular substance, but in Children are so near together that the intercellular substance only represents narrow reticulated cords between the cells, causing in this way an appearance similar to epithelium. In approaching the equator of such a sphere, cells become visible which show angular contours and short single outrunners. Further on, the cartilage cells are multipolar, the single outrunners are proportionately very long, branched, and anastomose with one another. Proceeding in this way so far as the insertion of the capsule, we encounter a zone where the cartilage cells gradually pass over into connective tissue cells. Böhm has laid great weight on the bearing this circumstance has upon our conception of the serous canaliculi. I wish merely to call to mind the fact (in opposition to Böhm) that the appearance of the stellate cartilage cells is associated with proximity to the insertion of the synovial membrane, and not with mechanical relations of the cartilage (absence of rubbing, etc.).

Here we encounter the synovial membrane, for we immediately perceive vessels, some forming arcades and others penetrating downwards and enclosing the serous canaliculi between their meshes. It is impossible, however, to detect any lamina of cells overlying them. It is only at the point where the synovial membrane, as a distinctly recognizable sheath, leaves the cotyla and passes over the head of the joint that the superficial epithelial-like tracings become apparent.

Still we find in synovial membranes a zone, the zone of attachment, which in one direction forms a gradual transition into cartilage and in the other into a serous membrane. The question now arises whether outside of this zone, or, stating it more distinctly, whether between the two zones of attachment (since the synovialis is stretched out between two lines of bones), the membrane retains the character of a serous membrane, in a strict sense. Whether we find the differences important enough to separate the synovial

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* Loc. cit. p. 43.

membranes from the serous depends upon the way in which we look at the matter.

The following points of differentiation present themselves: first of all, we recognize in the most successful preparations of synovial membranes that the framework of cementing substance does not always present such delicate, uniformly broad lines as the serous membranes; further, that the size and configuration of the cells and character of their nuclei vary more considerably in the former than in the latter; secondly, we find in most joints and in many sheaths of tendons villosities. I have also made similar observations in the articulations of new-born Children. Hüter has given another differential point, viz.: that the vessels of the synovial membrane lie naked. This distinction would certainly be of diagnostic importance; but Hüter's statement is not thoroughly correct. Where the stratum of overlying cells lies upon the serous canaliculi they are extended over the vessels; and yet, as it seems to me, Hüter's statement that the cells under discussion were to be separated from the endothelia was chiefly based on the ground that in the Frog, where the endothelia are so developed, similar cells do not appear on the inner side of the articulation, but cells whose entire character harmonizes with the epithelial cells of Mammals.

Böhm has further pointed out that in the serous membranes proper the epithelial layer never overlays fat when it occurs, while in synovial membranes it does so; he also mentions the circumstance that the superficial cells cannot be pencilled off with the brush. As for the first of these points it must be remembered that the endothelial tracings extend over the fat-cells. My statements are as follows:—

In opposition to Hüter; that the synovial membrane of joints has two layers, one of overlying cells and another of serous canaliculi.

In opposition to Böhm; that the cells of the former layer are nucleated.

In opposition to Schweigger-Seidel; that the arrangement and configuration of the nuclei corresponds in exceptional instances only with his drawings.

The relation between articular membranes and ligaments is curious, as shown in the knee, shoulder, and hip-joints. None of the ligaments on the side turned toward the articular cavity, where one would naturally expect a separation from the synovial membrane, have any covering of epithelial cells. On the contrary, the surfaces show the same markings as on the surface of the tendons, when they lie free in their synovial sheath. The view that a closed sac invests the entire cavity of the joint, is not correct.

The layer of serous canaliculi in the synovialis is remarkable for extreme richness in these channels.

That it contains cells, or, perhaps more properly, nuclei, is shown by employing the gold or chromic acid method; still it is somewhat difficult to obtain convincing proof. The form of these plasmatic channels embraces various types.

Böhm was the first who claimed for the blood-vessels that they open into the serous canaliculi, and that the spaces in which the blood-vessels lie actually communicate with the serous canaliculi.

Hüter asserted that he had never observed such conditions in the lymphatic system; that only in inflammation, when the tension of the subsynovial lymph-paths becomes considerable, occurrences of this kind sometimes exist. Landzert, on the other hand, states that by employing his silver-method the lymphatics are brought into distinct view.

I have not had similar success. Once only, in the knee-joint of the Hog, I found distinct tapering lymph-spaces closed with endothelium, and covered

by an epithelial layer. Spaces with similar outlines are also frequently found in Man, but I have never yet succeeded in discovering endothelia in them. It is possible that some of them were lymphatic vessels, but this much is certain, that most of these clear spaces are only depressed folds in which the silver does not penetrate. The folds rise into marked prominence by the silver method, and it is demonstrable that the white spaces resembling lymphatics only correspond to the folds that are seen with the naked eye.

The synovial membranes of the sheaths, objects easily examined, have the following structure: The basis structure of the duplicatures is formed of fibrillated connective tissue, in which cartilage-cells are embedded at certain regular points. Above are the serous canaliculi preserving the same arrangement and form as in the articular membranes; in some places the network of the basis substance is so narrow as to recall to our mind epithelial formations. Closer examination, however, teaches that the same relations exist here as in the zones of attachment of the articular synovial membrane. The structures under discussion lie in the same plane with the most clearly-marked branching figures, and one can easily see how the lines of the basis substance widen and form a gradual transition into broad colored fields of the same substance. Apart from the cartilage-cells, the lamellæ passing over to the tendon as meso-tendons have the same structure.

Finally, the inner wall of the fibrous sheath has the same structure as the surface of the tendons; and in alluding to the latter, I could only repeat what Von Recklinghausen has stated.

The inner wall of the typical mucous cyst, too, of which I examined several in Man, presents the same structure; the same is true, too, of congenital mucous cysts, as far as can be stated with probability, relying upon but a simple observation.

Since the latter are clearly developed out of interspaces in connective tissue, we have perceived that in the synovial cavities there is really a transition from simple connective-tissue meshes to such highly organized cavities that they rank next in order to the serous ones.

II. On the Non-pedunculate Hydatids.

By Dr. ERNST FLEISCHL.

The following anatomical facts may be regarded as definitely ascertained from what has been regarded as a thorough investigation into the structure of this body. They are as follows, viz. :—

In the furrow between the testicle and head of the epididymis, an organ is observed in Man which never reaches a greater size than two peas, nor is ever entirely absent; it was formerly described and well known as "Morgagni's Non-pedunculate Hydatid," and was held by Krause as the analogue of the intestinal appendix epiploica.

This structure, consisting of nucleated connective tissue, and traversed by nerves, blood-vessels, and broad lymph-spaces, is clothed superficially with a layer of ciliated epithelium, which extends also into the broad sacculated depressions of the surface, which are very numerous, and extend from the very apex of the organ into its interior. At the base of the organ a continuous, mostly irregular line extends, which is frequently to be seen by the naked eye, and represents the boundary between the proper epithelium of the mucous membrane and the serous flattened epithelium (endothelium) of the visceral layer belonging to the tunica vaginalis propria, just as in the

free border of the abdominal mouth of the Fallopian tube, or at the base of the ovary, a line forms a sharp boundary between the peritoneal and germinal epithelium. Further, near the base of the organ a canal commences, for whose uniform existence, however, I cannot vouch, but which extends towards the tunica albuginea testis, and occasionally even penetrates deep into its substance.*

The wall of this canal consists of the following coats: First of all comes a cylindrical tube of closely-knit, generally circular connective-tissue fibres; then follows a thick lamina of loose connective tissue, which rises into the lumen as broad prominent longitudinal ridges, which in the axis of the canal almost touch by their summits, and form between them deep depressions; most internally there is a layer of cylindrical epithelium, which very probably supports ciliæ. The analogy of this entire apparatus with those portions of the female organs which are developed out of the upper end of the layer of germinal epithelium is a clear one, and the microscopical sections of this canal and of the tube are so similar that they may easily be mistaken one for the other.

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* I did not mention this canal in my previous article on "The Non-pedunculate Hydatids (Centralbl. 1871, No. 9), though I knew of it at that time. Soon after publishing this article, however, Professor Waldeyer was kind enough to acquaint me by letter with his views as to the significance of the organ, which he himself had examined in the mean while. This letter contains, among other things, a most minute description and highly probable explanation of the nature of the canal.

ADDENDA.

Page 514. In the "pricking method" or method of "injection by puncture" (*vide* chap. xxxvi. ; viii., page 937), a cataract needle is inserted beneath the surface and pushed obliquely forwards until it reaches the region whose lymph-vessels it is intended to inject; the needle is then withdrawn and the delicate nozzle of the syringe is made, by a gentle rotatory motion, to follow the same track. Instead of a ligature the tissues around the point of entrance of the nozzle may be pressed firmly against the latter by the fingers. In this way the injected material, cautiously driven out under a steady but moderate pressure, *often* finds its way into the wounded lymph-vessels of the part. (For details in regard to this process, consult Frey's Histology and Technology.)

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